Mollusks of the Colorado River Corridor
Grand Canyon, Arizona

Including an Overview of Mollusks of the Grand Canyon Region

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ABSTRACT

Aquatic and terrestrial mollusks of the Colorado River corridor through the Grand Canyon, Arizona, occupy an uncertain position in the trophic food web of the region. In the river corridor, mollusks are probably taxonomically diverse, but their habitats are restricted to tributaries. Aquatic mollusks are known in the Colorado River itself only in the fishery between Glen Canyon Dam and Lees Ferry; limnological constraints, primarily sedimentation, preclude their colonization of the river below Lees Ferry. Aquatic mollusks of the river corridor are represented principally by *Physella* spp. (Physidae). In the river corridor this group may be mixed descendents of native populations and individuals introduced to the Lees Ferry fishery in the 1960s. Distribution of this group appears to be mostly by the mechanism of downstream transport in the Colorado River, whose frequent dam-controlled inundation of tributary mouths provides for the redeposition of individuals and egg masses in these habitats. Terrestrial mollusks in the river corridor are, with the singular exception of Vasey's Paradise, found only in tributaries above the high water zone of the Colorado River; they have not thusfar been located along the Colorado River even in favorable habitats established in the post-dam riparian regime. Comparable habitats of Thunder River host diverse taxa in a riparian environment that provides an indication of the potential for terrestrial molluscan habitation of the riparian environment of the Colorado River. Included in the Thunder River community are mixed taxa representative both of the inner canyon and surrounding plateaus; some are significantly displaced from their normal altitudinal distributions. The effects of the river on productivity of the mollusks of the inner canyon are unknown. No previous baseline study of the mollusks is available for the river corridor, and molluscan studies of the Grand Canyon region are not substantially more advanced than they were 80 years ago. This study reports ten species as new records of occurrence in the Grand Canyon; of these, three species are new records of occurrence in the Grand Canyon region, and two are new records of occurrence for the state of Arizona. One taxon particularly, *Oxyloma* cf. *haydeni* (Binney, 1858) records a genus previously unknown alive in Arizona (rather only as fossils), and the species could be new to science; the only colony thusfar known in Arizona lives at Vasey's Paradise. The Colorado River does not appear to be a barrier in the biogeographic range of any of the species found during the reconnaissance reported here, although the Grand Canyon region is the biogeographic boundary for some taxa. A significant amount of work remains to be done toward understanding the trophic position of the malacofauna in the Grand Canyon. The inner canyon provides a unique area to study the taxonomic diversity and seasonal production of native and introduced species in a protected wilderness hosting multiple life zones.

INTRODUCTION

A reconnaissance of mollusks of the Colorado River corridor was made in the summer of 1991 through most of the Grand Canyon (including Marble Canyon), Arizona. Between Lees Ferry and Diamond Creek, a distance of 225 miles along the river, 43 sites were examined for aquatic and terrestrial mollusks (Table 1). In this report, the Colorado River corridor includes the lower reach of tributaries. The Grand Canyon, Arizona Strip north of the canyon, and extreme southern Utah delineate the northern limit of the Southwestern Molluscan Province (Bequaert & Miller, 1973; Burch & Pearce, 1990).

NOTE ADDED IN PROOF: Re-collected specimens of slugs from Thunder River have been identified as the cosmopolitan species *Deroceras laeve* (Müller, 1774) (Limacidae) (*teste* K. C. Emberton). Specimens ANSP A16167.

Table 1. List of localities examined in 1991 for aquatic and terrestrial mollusks.

Localities in **bold print** yielded molluscan specimens.

Mile and Bank		Locality[1]	Months of Examination[2]
0.0	R	**Lees Ferry**	March, May, July, November
30.2	R	Fence fault camp	July
31.8	R	**Vasey's Paradise**	June, July, September
41.0	R	Buck Farm Canyon	June
44.5	L	Willie Taylor camp	May
47.0	R	**Saddle Canyon**	May, July
52.1	R	**Nankoweap Creek**	July
52.6	R	Nankoweap middle camp	July
56.0	R	Kwagunt Creek	July
61.2	R	Little Colorado camp	July
61.4	L	Little Colorado River	May, June, July
65.5	R	Lava Canyon	July
74.5	R	Below Mile 74.4 camp	July
81.2	L	Grapevine Rapids camp	July
87.0	L	Cremation fault camp	July
87.8	R	**Bright Angel Creek**	July
95.0	L	**Hermit Creek**	July
97.8	R	Upper Crystal camp	July
98.1	R	Crystal Creek	July
108.8	R	Shinumo Creek (below falls)	June
		Shinumo Creek (above falls)	July
116.6	L	**Elves Chasm**	May, June, July
120.1	R	**Blacktail Canyon**	May, September
131.8	R	Stone Creek	July
133.5	R	First Tapeats camp	July
133.7	R	Tapeats Creek (mouth)	July
		Tapeats Creek (upper)	July
		Thunder River	July
136.1	R	Deer Creek (river area only)	May, June
143.4	R	**Kanab Creek**	July
150.3	L	Upset camp	July
151.5	R	The Ledges	May
156.8	R	Havasu Creek	June, August
164.5	R	**Tuckup Canyon**	May
166.4	L	National Canyon	August
168.0	R	Fern Glen	August
177.1	L	Honga Spring camp	August
179.4	L	**Lava Falls Spring**	August, September
203.3	R	Mile 203.3 camp	August
204.3	R	**Spring Canyon**	August
212.9	R	Spring opposite Pumpkin Springs	August
224.5	L	Diamond Peak camp	August
225.7	L	Diamond Creek	August

[1] Nightly campsites represent casual observations only; camp names are informal based on geographic or historical features nearest campsites marked in Stevens (1987).

[2] Includes months during which collections were made by others, with specimens sent to the senior author.

Virtually no data exist about mollusks from previous surveys of the Colorado River and tributaries in the Grand Canyon, and there are no data at all about river corridor mollusks in literature published before the 1963 closure of Glen Canyon Dam. In fact, only one original publication is available on mollusks of the Grand Canyon region (Pilsbry & Ferriss, 1911); the more recent review of Arizona mollusks by Bequaert & Miller (1973) for the most part repeats the Grand Canyon regional data published by Pilsbry & Ferriss. Neither publication addresses the Colorado River corridor in the Grand Canyon. Thus the data obtained by the 1991 reconnaissance constitute a benchmark, to which future investigations will be compared in order to make interpretations for biological research or river management decisions.

We provide more background data than would be called for if previous work were available. Some of our findings present new information on zoogeography of molluscan species, including new records of occurrence for the Grand Canyon, the Grand Canyon region, and Arizona. We emphasize the pioneering nature of this study and regret that interpretations that would be made through comparisons with previous studies are not forthcoming. Some of our interpretations are necessarily conjectural, due also to uncertainties about specific requirements and habits of the mollusks. There likewise are many questions which remain unanswered at this time. For these reasons, suggestions for future work are added to this report.

All collected specimens are available for research (Table 2) and represent the only available collection of mollusks from the Colorado River corridor in the Grand Canyon. They have been computer-cataloged into the collections of the Department of Malacology at the Academy of Natural Sciences of Philadelphia.

PREVIOUS WORK

Previous work on Grand Canyon mollusks is restricted to three general areas: the cross-canyon survey published by Pilsbry & Ferriss (1911), sporadic single notes of occurrence, and casual reports of mostly unidentified mollusks in recent biological studies of the Colorado River and tributaries. Only the recent studies, restricted to the river corridor, discuss in any detail the ecological conditions under which the mollusks live.

Taxonomic Work

The first record of Grand Canyon mollusks is Stearns' (1890:206, pl. 25, figs. 6-8) description of *Helix* (*Arionta*) *coloradoensis*, placed later by Pilsbry (1900) in the genus *Sonorella* Pilsbry, 1900. The published locality is only "Grand Cañon of the Colorado, opposite the Kaibab plateau, at an elevation of 3,500 feet." The type specimen (USNM 104100) was taken by C. Hart Merriam, during his celebrated 1889 reconnaissance of northern Arizona life zones (Merriam, 1890), along what later would be Hance Trail (Merriam, 1890:4; Pilsbry, 1939:338-339).

In 1906, Henry A. Pilsbry and James H. Ferriss arrived at the Grand Canyon. Disembarking at the Bass Station flag stop on the Grand Canyon Railroad, just south of the canyon, they immediately collected snail specimens before being taken to the visitor accommodations run by William Wallace Bass, west of present-day Grand Canyon Village. Between 16 and 29 October 1906, Pilsbry and Ferriss traversed the Grand Canyon on Bass Trail from Bass Camp to the Kaibab Plateau, with a side trip to Mount Trumbull, ending the journey with a day on Bright Angel Trail (H. A. Pilsbry field notes, Department of Malacology, Academy of Natural Sciences of Philadelphia). They collected snails at more than 100 localities, many of which were revisited when Ferriss and L. E. Daniels repeated the cross-canyon journey in 1909 and continued

Table 2. List of cataloged lots of specimens collected during the 1991 reconnaissance. All lots have been deposited in the Department of Malacology, Academy of Natural Sciences of Philadelphia.

Taxon	Lot catalog numbers[1]
BIVALVIA	
VENEROIDA	
SPHAERIIDAE	
Pisidium variabile Prime, 1852	391072, 391073
Pisidium walkeri Sterki, 1895	A16155, A16156
GASTROPODA	
BASOMMATOPHORA	
LYMNAEIDAE	
Fossaria obrussa (Say, 1825)	A16162-A16163; 391079
PHYSIDAE	
Physella sp.	A16148-A16151, A16153, A16154, A16178-A16210, A16212; 391066, 391071, 391074, 391075, 391084
BASOMMATOPHORA INDET. (protoconchs only, ?PHYSIDAE)	A16160
STYLOMMATOPHORA	
COCHLICOPIDAE	
Cionella lubrica (Müller, 1774)	A16161; 391076
PUPILLIDAE	
Gastrocopta pellucida (Pfeiffer, 1841)	391080
DISCIDAE	
Discus cronkhitei (Newcomb, 1865)	391081, 391082
SUCCINEIDAE	
Catinella avara (Say, 1824)	A16211
Oxyloma cf. *haydeni* (Binney, 1858)	A16168-A16171; 391067, 391069, 391083, 391093, 391094
Succinea grosvenorii (Lea, 1864)	A16152, A16172-A16177; 391068, 391085, 391087, 391096-391099; fossils or subfossils: 391070, 391086, 391095
ZONITIDAE	
Glyphyalinia indentata (Say, 1823)	391078
Hawaiia minuscula (Binney, 1841)	A16164-A16167
Zonitoides arboreus (Say, 1817)	391077
OREOHELICIDAE	
Oreohelix strigosa (Gould, 1846)	A16157; 391090-391092
HELMINTHOGLYPTIDAE	
Sonorella coloradoensis (Stearns, 1890)	391088, 391089
STYLOMMATOPHORA UNDET.	
slugs, ?LIMACIDAE	A16158, A16159

[1] Numbers with the "A" prefix are alcohol-preserved lots; other numbers are dry lots. Institutional acronym is ANSP.

to Utah. Pilsbry & Ferriss (1911) published their identifications in what remains the only comprehensive account of mollusks of the Grand Canyon region, updated in part in Pilsbry's (1939-1948) monograph on American land snails north of Mexico, and in part by Bequaert & Miller (1973). Pilsbry & Ferriss (1911) described 42 species and subspecies, including five new species-level taxa. The specimens from Pilsbry's and Ferriss' collecting trips are held in the Department of Malacology at the Academy of Natural Sciences of Philadelphia; information on these lots have been added to the department's computerized database.

Daniels (1911) published notes on gravid females of *Oreohelix* taken during his 1909 Grand Canyon trip with Ferriss. In 1912, Daniels published a paper on abnormal shells, including therein some brief remarks on Grand Canyon shells of *Sonorella coloradoensis* and *Oreohelix strigosa depressa* (Cockerell, 1890) [= *O. strigosa* (Gould, 1846)].

Henderson (1914) described the new species *Sonorella betheli*, said to be from the Bright Angel Trail. However, Pilsbry (1938:172) indicated that the locality information was in error, that the specimen probably was from Los Angeles, California. He synonymized the species with *Helminthoglypta traski* (Newcomb, 1861).

Cockerell (1927) published a note on fossil or subfossil shells of a large form of *Oreohelix yavapai* Pilsbry, 1905, from the Bright Angel Trail. For them he erected the subspecies *O. y. fortis*, and he indicated that it was "closely related" to *O. y. angelica* Pilsbry & Ferriss, 1911, found living near the top of Bright Angel Trail. Both subspecies are synonyms of *O. yavapai*, a species named from animals first described from Oak Creek Canyon, Coconino County, Arizona.

Marshall (1929:1-2, pl. 1, figs. 1-3, 11) described the new fossil or subfossil subspecies *Oreohelix yavapai vauxae* (= *O. yavapai*), found at Supai, Havasu Canyon.

Miller (1984) is the only contemporary author to have published on any Grand Canyon mollusk. He described the new species *Sonorella reederi* based on animals found just west of Rampart Cave, in the westernmost part of the Grand Canyon. This record constitutes the only previous publication of a specifically identified mollusk from the Colorado River corridor.

Bioecological Work

Pilsbry & Ferriss (1911) published useful information on the ecology of some of the mollusks they found in the Grand Canyon. However, no collections were made in the river corridor in the area where they crossed the Colorado on Bass's cable car. One of Ferriss' 1909 collection stations was in "the box" of Shinumo Canyon, which constitutes the only station in immediate communication with the river corridor.

Environmental concerns have in recent years instigated studies of the biotic communities of the Colorado River corridor through the Grand Canyon. Contracted and other commissioned reports summarize the data obtained by field investigators and provide interpretations of the impact that man has had on the river corridor (e.g., Carothers & Minckley, 1981; U.S. Department of the Interior, 1988; U.S. National Research Council, Committee to Review the Glen Canyon Environmental Studies, 1987; and Carothers & Brown, 1991). The biological aspects of these reports have concentrated on plants, mammals, lizards, birds, aquatic insects, and chemical properties of the waters of the Colorado River and wet tributaries. The malacofauna has, if mentioned at all, been included only under generalized categories—"mollusks," "snails," or if systematic names are used, usually only to family level, occasionally to misidentified genus, and never to species.

Cole & Kubly's (1976) pioneering survey of the limnology of the Colorado River lists *Physa* (actually *Physella* [Physidae]) and *Lymnaea* (Lymnaeidae). They reported (p. 83) both genera from the "Colorado River" (at Lees Ferry, see their p. 39), only *Physa* at Elves Chasm and Havasu Creek, and only *Lymnaea* from Vasey's Paradise. The identification of *Lymnaea* at Vasey's Paradise might be incorrect; they could have seen what is reported here as *Oxyloma* cf. *haydeni* (Binney, 1858).

The overview of Colorado River biotic resources by Carothers & Minckley (1981) cites only "Physidae adults" as a minor component in the diets of some fish, and "Physidae" and "Lymnaeidae" in a checklist of aquatic invertebrates (pp. 90, 92-93). These authors cited Pilsbry & Ferriss (1911), mentioning that *Physa gyrina* and *P. humerosa* had been identified at Kanab Creek and Indian Gardens (Bright Angel Trail), respectively; but they did not mention that Pilsbry & Ferriss' Kanab Creek locality was six miles above Kanab, Utah, not in the Grand Canyon. And no specific or generic identifications were made of the Colorado River specimens they encountered. As the most comprehensive previous survey that mentions the distribution of mollusks of the river corridor, we compare the records of Carothers & Minckley with the distributions reported here (Table 3).

Maddux et al. (1987:167) listed under "Mollusca" only "Undetermined species" in their census of organisms taken from plankton tows in the Colorado River. In their description of fish food resources (pp. 165-178), "molluscs" are included in volumetric analyses of fish gut contents, without further elaboration.

Tomko (1976:48-49) reported that the gut contents of the lizard *Cnemidophorus tigris* included "snails." His only remark was that the lizard is a forager frequenting the water's edge, "and it is quite likely that the aquatics were taken from very shallow (<5mm) pools created by the daily ebb of the Colorado River" (p. 48).

Information on the biotic resources of the Colorado River prior to the closure of Glen Canyon Dam in 1963 is scant, with much of existing knowledge of it reconstructed from nontechnical as well as technical publications on various subjects. Post-dam ecological studies have information mostly with reference to plants, vertebrates, and aquatic insects. Malacofaunal data of the pre-dam river corridor are non-existent, a usual oversight of early ecological studies most everywhere. For example, a valuable report edited by Woodbury (1959) examines the vegetational and faunal resources of Glen Canyon in the area to be inundated by the Glen Canyon Dam reservoir. The only note therein of mollusks is (p. 174): "One [fish] stomach contained fragments of a bivalve shell, a mollusk known from the headwaters of tributary streams." (It is interesting to point out that this is the only mention of bivalves in the Colorado River literature referred to for this study. All other references have been to gastropods.)

After the closure of Glen Canyon Dam, the Arizona Game and Fish Department established a fishery, primarily for trout, in the tailwaters between the dam and Lees Ferry. It has been a successful recreational resource, although a resource quite artificial in faunal content. To establish this fishery, food resources were introduced to the river between 1966 and 1969 (Stone & Queenan, 1967; Stone & Rathbun, 1968, 1969). In addition to worms, crustaceans, and aquatic insects, 50,000 snails were introduced to three sites in the fishery—Lees Ferry, 5 Mile Bend, and the West Diversion Tunnel below the dam. The snails were collected from tailwaters of Navajo Dam, on the San Juan River in New Mexico. Stone & Queenan (1967:18) list the snails as *Physa* and *Stagnicola*, but the reports by Stone & Rathbun (1968, 1969) mention only *Physa*. The snails identified as *Physa* are probably *Physella* because this is the genus of native North American physids (Burch, 1989), and those identified as *Stagnicola* are probably *Fossaria* because *Stagnicola* does not occur in the Southwestern Molluscan Province (Bequaert & Miller, 1973; Burch & Pearce, 1990). Some shells of *Fossaria* can be confused for *Stagnicola*. As is mentioned later in this report, the successful introduction of

Table 3. Mollusk-bearing sites in the Colorado River corridor, Grand Canyon, reported in the survey by Carothers & Minckley (1981) and the 1991 reconnaissance.

Identifications are at the family level to facilitate comparison of the 1991 reconnaissance with the data reported by Carothers & Minckley (1981). An "x" indicates specimens of that family reported from the locality; a dash (—) indicates no specimens reported; "not examined" indicates that the locality was not visited by the cited authors.

Mile and Bank		Localities Examined (**bold print** indicates mollusks found)	Carothers & Minckley (1981)		This Report		
			Physidae	Lymnaeidae	Physidae	Lymnaeidae	Others
0.0	R	**Lees Ferry**	—	—	x	—	x
0.0	R	Paria River	—	—	Not examined		
31.8	R	**Vasey's Paradise**	—	x	x	x	x
41.0	R	Buck Farm Canyon	—	—	—	—	—
47.0	R	**Saddle Canyon**	Not examined		—	—	x
52.1	R	**Nankoweap Creek**	—	—	x	x	x
56.0	R	Kwagunt Creek	Not examined		—	—	—
61.4	L	Little Colorado River	—	—	—	—	—
65.5	R	Lava Canyon	Not examined		—	—	—
72.6	R	Unkar Creek	—	—	—	—	—
84.1	R	Clear Creek	—	—	—	—	—
87.8	R	**Bright Angel Creek**	x	—	x	—	—
88.9	L	Pipe Creek	—	—	Not examined		
95.0	L	**Hermit Creek**	x	—	x	—	x
98.1	R	Crystal Creek	—	—	—	—	—
108.8	R	**Shinumo Creek**	—	—	—	—	x
116.6	L	**Elves Chasm**	x	x	x	—	—
120.1	R	**Blacktail Canyon**	Not examined		x	—	—
131.8	R	Stone Creek	—	—	—	—	—
133.7	R	Tapeats Creek[1]	—	—	—	—	—
136.2	R	**Deer Creek**	x	—	—	—	—
143.4	R	**Kanab Creek**	—	—	x	—	—
155.5	R	The Ledges	Not examined		—	—	—
155.7	R	155 Mile Creek	—	—	Not examined		
156.8	L	**Havasu Creek**	x	—	—	—	—
164.5	R	**Tuckup Canyon**	Not examined		x	—	—
166.4	L	National Canyon	—	—	—	—	—
179.4	L	**Lava Falls Spring**	x	—	x	—	x
190.3	L	190-1/2 Mile Creek	—	—	Not examined		
204.3	R	**Spring Canyon**	Not examined		—	—	x
212.9	R	Spring opposite Pumpkin Springs	Not examined		—	—	—
215.7	L	**Three Springs Canyon**	x	—	Not examined		
219.2	R	Trail Canyon[2]	—	—	Not examined		
225.7	L	Diamond Creek	—	—	—	—	—
229.0	L	Travertine Canyon	—	—	Not examined		
230.5	L	Travertine Falls	—	—	Not examined		
235.0	L	Bridge City	—	—	Not examined		
235.2	L	**Bridge Canyon**	x	—	Not examined		
Lake Mead							
246.0	L	Spencer Canyon	—	—	Not examined		
275.0	L	**Near Rampart Cave**[3]	Not examined		Not examined		

[1] Mollusca of several families are reported herein from upper Tapeats Creek and Thunder River.
[2] 219 Mile Canyon of Carothers & Minckley (1981).
[3] Miller (1984) reported a new species of *Sonorella* (Helminthoglyptidae) from this locality, included here for completeness.

these snails has uncertain implications toward distinguishing the natural fauna of aquatic mollusks in the Colorado River corridor through the Grand Canyon.

FIRST MALACOLOGICAL RECONNAISSANCE IN THE RIVER CORRIDOR

The senior author joined a Glen Canyon Environmental Studies research trip on the Colorado River from 24 July to 4 August 1991, from Lees Ferry (Colorado River Mile 0.0) to Diamond Creek (Mile 225.7). With the exception of Lees Ferry, mollusks have not been seen in the Colorado River itself (although the report by Maddux et al., 1987, included note of undetermined mollusks taken in plankton tows; these may have washed in from tributaries). At all stops, searches were made for terrestrial snails, either alive or dead. These examinations were made at cliff bases, in vegetational debris, shallowly around roots of plants, and along dry and wet streamcourses. Aquatic mollusks were sought in all wet tributaries that were visited; examination sites were in streamcourses, pools, and pools isolated by ebbing stream levels. Dried pools and banks of ebbing streams were examined for dead stranded mollusks. Where ebbing river levels left pools at and near the mouths of tributaries, these pools also were examined.

As the first reconnaissance for mollusks in the river corridor, with no previous records of habitat, all habitats at each stop were at least casually examined. Since terrestrial snails had never been reported from the river corridor, a special effort was made to find them, and nightly campsites were included among the localities to be searched (done in day- and twilight). However, time constraints precluded the tedious process of quarrying talus (particularly limestone talus) for some species of land snails. It is likely that the data about terrestrial mollusks reported here do not reflect their true distribution/abundance profile in the river corridor because of uncontrolled collecting conditions, variable search times, and logistics. The abundance of species at Vasey's Paradise (Mile 31.8) is an indication of the potential for species abundance in the river corridor.

One investigative survey was made away from the Colorado River corridor, at Thunder River, a tributary of Tapeats Creek. The ecology of Thunder River is a rich riparian one in an otherwise semiarid life zone. It hosted the most diverse assemblage of terrestrial mollusks encountered during the reconnaissance—eight species in seven families. The species assemblage there can be used as an indicator of potential habitation of ecologically favorable sites in the river corridor. Noticeably absent during the brief survey there were aquatic mollusks, even though the site is perennially wet. The fast-flowing water and steep grade of Thunder River may prohibit occupation by aquatic mollusks (if they are in fact absent there). Tapeats Creek (Mile 133.7), the lower-grade drainage into which Thunder River flows, does host aquatic mollusks as indicated by Carothers & Minckley (1981); the senior author found none at several points examined between the Colorado and Thunder rivers, but one specimen of a terrestrial gastropod was found.

We stress the preliminary nature of this reconnaissance. A number of constraints influenced the number of taxa and specimens that were collected: the number of localities visited (the malacological investigation was only a part of a more wide-ranging biological survey), the area covered and the number of potential habitats at each locality, and the length of time allowed at each stop or in travel to specific sites not by the river. The number of specimens of each taxon collected is itemized in Table 4; search times with tallies of the number of taxa and specimens collected are itemized in Table 5. Empirically, one will find additional taxa when more time is spent at localities, and when localities are revisited (e.g., Tillier, 1989; and here: specimens of *Succinea grosvenorii* (Lea, 1864) from Lava Falls Spring [Mile 179.4] were sent by another collector; the taxon had not been seen by the senior author while at that locality). The results reported here are a first look at an unexamined aspect of the Grand Canyon ecosystem. The interpretations that we make are presented as a framework for future research; they are based partly on an admittedly unclear

Table 4. Number of specimens of mollusks collected in the Colorado River corridor and at Thunder River, Grand Canyon, during the 1991 reconnaissance.[1]

Taxon[2]	Ecology	No. of Specimens: River Corridor	Thunder River	Total
BIVALVIA				
VENEROIDA				
SPHAERIIDAE				
Pisidium variabile Prime, 1852	Aquatic	4		4
Pisidium walkeri Sterki, 1895	Aquatic	3		3
GASTROPODA				
BASOMMATOPHORA				
LYMNAEIDAE				
Fossaria obrussa (Say, 1825)	Aquatic	3		3
PHYSIDAE				
Physella spp.	Aquatic	996		996
STYLOMMATOPHORA				
COCHLICOPIDAE				
Cionella lubrica (Müller, 1774)	Terrestrial		17	17
PUPILLIDAE				
Gastrocopta pellucida (Pfeiffer, 1841)	Terrestrial	1		1
DISCIDAE				
Discus cronkhitei (Newcomb, 1865)	Terrestrial		6	6
SUCCINEIDAE				
Catinella avara (Say, 1824)	Terrestrial	6		6
Oxyloma cf. *haydeni* (Binney, 1858)	Terrestrial	83		83
Succinea grosvenorii (Lea, 1864)	Terrestrial	39	17	56
ZONITIDAE				
Glyphyalinia indentata (Say, 1823)	Terrestrial		1	1
Hawaiia minuscula (Binney, 1841)	Terrestrial	70		70
Zonitoides arboreus (Say, 1817)	Terrestrial		1	1
OREOHELICIDAE				
Oreohelix strigosa (Gould, 1846)	Terrestrial		61	61
HELMINTHOGLYPTIDAE				
Sonorella coloradoensis (Stearns, 1890)	Terrestrial		2	2
STYLOMMATOPHORA UNDET.				
slugs, ?LIMACIDAE	Terrestrial		4	4
TOTAL		1205	109	1314

[1] This list is a tally of specimens collected and is not useful for statistical interpretations of actual abundance. Also, in addition to the totals presented here there are four specimens in the collection that are protoconchs of undeterminable gastropods. Terrestrial taxa reported from the river corridor were, with the exception of Vasey's Paradise, collected in tributaries and not along the river banks.

[2] Binomial and higher taxa follow the convention of Turgeon et al. (1988).

Table 5. Search times and numbers of mollusks found during the 1991 reconnaissance.[1]

Locality (bold print indicates mollusks found)	Approx. Search Time (hr)	Number of Taxa[2]	Number of Specimens
Lees Ferry[3]	—	3	22
Vasey's Paradise	1.5	5	395
Saddle Canyon	1.5	1	28
Nankoweap Creek[4]	3.5	2	37
Kwagunt Creek	0.7	—	—
Little Colorado River	1.0	—	—
Bright Angel Creek	2.0	1	67
Hermit Creek	0.7	2	2
Crystal Creek	2.0	—	—
Shinumo Creek	0.7	1	6
Elves Chasm	1.5	1	240
Stone Creek	0.5	—	—
Tapeats Creek (mouth)	0.3	—	—
Tapeats Creek (upper)	0.2	1	1
Thunder River	1.0	8	109
Blacktail Canyon	0.2	1	7
Kanab Creek[4]	1.0	1	57
Havasu Creek	0.5	—	—
Tuckup Canyon	0.3	1	9
National Canyon	1.0	—	—
Fern Glen	0.5	—	—
Lava Falls Spring	1.5	2	270
Spring Canyon[4]	2.0	2	65
Spring opposite Pumpkin Springs	0.5	—	—
Diamond Creek	0.2	—	—
TOTAL	24.8	16[5]	1314

[1] Nightly campsites not included; these were casual observations. The number of specimens is not the number seen, but only the number collected. Only the actual amount of time searching is tallied, not the total time on site. The total times include unproductive search times in unoccupied habitats, thus there is no simple correlation between number of specimens collected and time spent searching.

[2] *Physella* spp. are treated here as one taxon; similarly the unidentified slugs from Thunder River are counted as one taxon. The unidentified basommatophorans are not included in the total of taxa.

[3] Locality collected by others, with specimens sent to the senior author.

[4] Although specimens were found, the search at this locality included a significant amount of unproductive time before specimens were found.

[5] From Table 2.

understanding of some biological factors of these animals, generally as well as their habits in the Grand Canyon.

IDENTIFICATION OF SPECIMENS

Mollusks collected during the 1991 reconnaissance were identified using published keys and descriptions and through comparison of specimens in the extensive collections of the Department of Malacology at the Academy of Natural Sciences of Philadelphia (ANSP).

Literature references used in the identifications are: SPHAERIIDAE: Burch (1975), BASOMMATOPHORA: Baker (1911), Burch (1989), STYLOMMATOPHORA: Pilsbry (1939-1948) and additional references on genera and species as cited below. ANSP specimens were also used to examine specific characters and their variations; specimens from the Grand Canyon region were preferred if they existed; all referred material is listed in Table 6. When the types of species were available in the Academy's collections, they, too, were used for the comparisons. For nomenclatural and systematic consistency with the malacological community at large, in this report we adopt the nomenclatural and systematic conventions established by Turgeon et al. (1988). In a few instances, familial and generic placements of identified specimens in the ANSP collection are different from the arrangement by Turgeon et al.

The systematics of speciation in the genus *Physella* are not well understood, and no contemporary work on them is available. Te's (1978) unpublished doctoral dissertation on the systematics of the Physidae serves as the most recent work on the subject; it is devoted primarily to anatomical and molecular analyses in its interpretation of systematic relationships within the family. Shell morphology in *Physella* is variable even within the concept of each species, thus it is not a reliable character for identification at the species level. The specimens collected from the Colorado River corridor through the Grand Canyon were compared to specimens of species of *Physella* recorded in the Grand Canyon region (Pilsbry & Ferriss, 1911) and Arizona (Bequaert & Miller, 1973). No invariable shell characters could be determined between the two groups, even between the shells identified by H. A. Pilsbry from the Grand Canyon, so the new material from the river corridor is not identified to species. The variation does appear to be significant enough to declare that multiple species exist in the Grand Canyon.

The identifications of *Oxyloma* cf. *haydeni* and of *Oreohelix strigosa* were determined by anatomical dissection of genitalia, by A. E. Bogan and K. C. Emberton, respectively. *Oreohelix strigosa* is recognized in the Grand Canyon region as *O. s. depressa* (Cockerell, 1890), the nominate *O. s. strigosa* (Gould, 1855) not occurring either in Arizona or in the Southwestern Molluscan Province (Bequaert & Miller, 1973). However, the subspecific characters are not recognized in the systematic collections of the Academy of Natural Sciences, so identification of this animal is simply to the species *O. strigosa*. The recognition of living *Oxyloma* is new for Arizona, until now known in the state only from fossils (Bequaert & Miller, 1973; Mead, 1991). Penial features are not precisely like those described for *O. haydeni* (Binney, 1858) (see Franzen, 1964) or its synonymous taxon *O. h. kanabensis* Pilsbry, 1948, but are less similar than the characters for the closely related *O. retusa* (Lea, 1834) as described by Pilsbry (1948) and compared by Franzen (1964). For this reason we compare *O. haydeni* to the Grand Canyon specimens. However, the Grand Canyon *Oxyloma*, thusfar found only at Vasey's Paradise, might also be a new species, and investigations of its characters are in progress.

Slugs from Thunder River decomposed prior to being preserved, and the remnants are unsuitable for identification. We tentatively refer them to the stylommatophoran family Limacidae. Specimens from a subsequent collection were not yet available to the authors at the time of this writing.

Table 6. Comparative material used in the identifications of Grand Canyon mollusks collected in 1991.

Taxon	Comparative Material[1]
SPHAERIIDAE	
Pisidium variabile Prime, 1852	TYPES, 59044 (Massachusetts); 132817 (Colorado)
Pisidium walkeri Sterki, 1895	87182 (Michigan)
LYMNAEIDAE	
Fossaria obrussa (Say, 1825)	TYPES, 58700, 329883 (Harrowgate [Philadelphia, Pennsylvania])
PHYSIDAE	
Specimens from the 1991 reconnaissance identified only as *Physella* spp. The following species were examined, but identifications of specimens based on shell characters are inconclusive (identifications as in collection of Academy of Natural Sciences):	
Physella bottimeri (Clench, 1934)	TYPES, 133511 (Stockton, Texas); 323667 (topotypes)
Physella gyrina smithiana (Baker, 1919)	103347 (Williams, Arizona)
Physella humerosa (Gould, 1855)	TYPES, 17279 ("Gran Jornado & Pecos River"); 104197 (Indian Gardens, Bright Angel Trail, Grand Canyon); 147018 (Griffiths Spring, Coconino County, Arizona)
Physella osculans (Haldeman, 1841)	79441, 143703 (Indian Gardens, Bright Angel Trail, Grand Canyon)
Physella propinqua nuttallii (Lea, 1864)	103315, 112305 (Kanab Creek, near Kanab, Utah); 112304 (Deception Lake, near Kanab, Utah); 143672 (Mormon Lake, Coconino County, Arizona)
Physella squalida (Morelet, 1851)	92102 (Indian Gardens, Bright Angel Trail, Grand Canyon)
Physella virgata virgata (Gould, 1855)	TYPES, 329442 (Gila River); 103314 (Pipe Spring, Arizona)
Physella virgata berendti (Fisher & Crosse, 1886)	143638 (Roosevelt Dam, Arizona)
Physella virginea (Gould, 1847)	17266, 110683 (California), 115182 (Nevada)
COCHLICOPIDAE	
Cionella lubrica (Müller, 1774)	94082 (Bright Angel Trail, Grand Canyon), 94083 (Bass Trail, Grand Canyon), 103342 (Indian Gardens, Bright Angel Trail, Grand Canyon), 371698 (near Bass Camp)
PUPILLIDAE	
Gastrocopta pellucida (Pfeiffer, 1841)	TYPES of synonym *G. hordeacella* (Pilsbry, 1890): 11588 (St. Augustine, Florida); 57853 (Fort Grant, Arizona); 60460, 68884, 391100 (New Braunfels, Texas); also 97435 (as *G. hordeacella*; Bass Trail, Grand Canyon)

Table 6 (cont'd)

Taxon	Comparative Material
DISCIDAE	
Discus cronkhitei (Newcomb, 1865)	TYPES, 332852 (Klamath Valley, California); 94078 (Bill Williams Mountain, Arizona); 104189 (Mount Trumbull, Arizona); 143650 (San Francisco Mountain, Arizona)
SUCCINEIDAE	
Catinella avara (Say, 1824)	TYPES, 59542 ("Northwestern Territory" [U.S.]); 94070, 105535 (Shinumo Creek, Grand Canyon); 103307 (Muav Creek, Grand Canyon); 103309 (Kaibab Plateau, Arizona); 144500 (Bass Trail, Grand Canyon); 144503 (White Creek, Grand Canyon)
Oxyloma haydeni (Binney, 1858)[2]	144621 (Lake Utah, Utah); 346355 (Weber Canyon, Utah). Also: TYPES, 103166 and 391101, of synonym *O. h. kanabensis* Pilsbry, 1948 (Kanab Creek, near Kanab, Utah)
Succinea grosvenorii (Lea, 1864)	103163 (Kaibab Plateau, Arizona), 147017 (Willow Spring, Navajo Indian Reservation, Arizona)
ZONITIDAE	
Glyphyalinia indentata (Say, 1823)	TYPES, 11954 (New Jersey); 94077, 144499 (White Creek, Grand Canyon); 104183, 104184 (Kaibab Plateau, Arizona); 143602 (Bright Angel Point, Grand Canyon)
Hawaiia minuscula (Binney, 1841)	TYPES, 74416 (Ohio and Vermont); 79412 (Oak Creek, Arizona); 103262, 103263 (Mount Trumbull, Arizona); 103264 (Bill Williams Mountain, Arizona); 324152, 324163 (San Francisco Mountain, Arizona)
Zonitoides arboreus (Say, 1817)	103261 (Bill Williams Mountain, Arizona), 144504 (White Creek, Grand Canyon); 324167 (San Francisco Mountain, Arizona)
OREOHELICIDAE	
Oreohelix strigosa (Gould, 1846)[2]	TYPE of *O. s. depressa* (Cockerell, 1890), 187457 (Colorado); and many lots in collection under that name
HELMINTHOGLYPTIDAE	
Sonorella coloradoensis (Stearns, 1890)	99170, 103338 (Powell Plateau, Grand Canyon); 103255, 103335 (White Creek, Grand Canyon; lot 103255 contains the specimens figured by Pilsbry & Ferriss, 1911, pl. 12, figs. 26-28), 103333 (Shinumo Canyon, Grand Canyon)
STYLOMMATOPHORA UNDET.	
?LIMACIDAE, gen. and sp. undet.	No comparisons made

[1] Catalog numbers are for lots in the Department of Malacology, Academy of Natural Sciences of Philadelphia. Type lots may consist of holotype, paratypes, or syntypes.

[2] Identification of 1991 Grand Canyon specimens based on published descriptions of anatomy; *Oxyloma* cf. *haydeni* by A. E. Bogan, *Oreohelix strigosa* by K. C. Emberton.

DISTRIBUTION AND HABITATS

Aquatic and terrestrial mollusks live in tributaries of the Colorado River throughout the Grand Canyon. Between Glen Canyon Dam and Lees Ferry abundant aquatic invertebrates and aquatic plants like the algal form *Cladophora* inhabit the river where it is mostly free of sediment (the natural sediment load of the river being deposited in Lake Powell, the impoundment behind Glen Canyon dam). Downstream from Lees Ferry, the abundance of aquatic invertebrates and algae rapidly decrease due to the impact of sediment loads added to the clear river from the Paria River (Mile 0.0) and other large tributaries downstream—Little Colorado River (Mile 61.4) and Kanab Creek (Mile 143.4) (see, for example, summary descriptions of these effects by Carothers & Brown, 1991). The impact on the malacofauna is more dramatic; no mollusks are known to live in the river itself below Lees Ferry, although, as we indicate here, they probably can survive for periods of time when washed into the river from tributaries.

No sites between tributaries were found to be inhabited by terrestrial species, and no previous records exist against which to compare these observations. Extensive searches, such as talus quarrying, were not undertaken due to time constraints. At two riverside springs—Vasey's Paradise and Lava Falls Spring—terrestrial gastropods have been taken; they live above the high water zone of the river. The distribution of mollusks taken during the 1991 reconnaissance is shown in Table 7. The most widely distributed species are the aquatic gastropod *Physella* spp. and the terrestrial gastropod *Succinea grosvenorii.*

The molluscan community at Thunder River is the most diverse community of localities visited during the 1991 reconnaissance. A correspondingly diverse molluscan community in the Colorado River corridor is Vasey's Paradise. The distribution of river corridor taxa found at few localities is probably a statistical artifact of non-collection; most are probably widely distributed, in addition to the likely presence of additional taxa.

None of the species described from the 1991 reconnaissance in the river corridor and at Thunder River are threatened or endangered. However, in some cases, most notably the occurrence of *Oxyloma* cf. *haydeni* at Vasey's Paradise, some taxa are at this time the only recorded populations inside the Grand Canyon (Table 7).

The life habits of many aquatic and terrestrial mollusks are not well understood, and published characteristics of their many ecological requirements are somewhat generalized. Many forms are sensitive to such environmental alterations as pollution and siltation, while others, such as the gastropod family Physidae, so well represented in the Grand Canyon tributaries, are somewhat more tolerant (Burch, 1989).

Aquatic Mollusks

The molluscan groups that are found in the Grand Canyon are functional elements in a complex ecosystem. Bivalve communities have not been discovered anywhere but in the fishery above Lees Ferry. The genus that is found there, *Pisidium*, is not a significant water filterer in terms of the biomass they represent. Although they are often found in silty waters, the sediment loads of the pre-dam Colorado River might have been sufficiently high to preclude their survival there. Unfortunately, no record is had of their existence or absence in the pre-dam river, so we are unsure whether they are native to this part of the river. The species of *Pisidium* reported here from the fishery are of unknown abundance; they may be accidental introductions, but, if not, they could have arrived through natural mechanisms of dispersal after the closure of Glen Canyon Dam. In either case they appear to inhabit an ecological niche not normal to them, and the population may be little more than self-propagating (but this remains to be determined). From a sample size of just seven specimens from Lees Ferry, two species of *Pisidium* are identified, *P. variabile* Prime, 1852, and *P. walkeri* Sterki, 1895. These are widely distributed North American species, but the presence of *P. variabile* is a new record of occurrence for Arizona. *P. walkeri* is said to be "scarce and usually not abundant in any one place" (Herrington, 1962:51, and quoted by Burch, 1975:41), usually occurring in small lakes and ponds. Both *P. walkeri* and *P. variabile* are found mostly in muddy bottoms; the Lees Ferry populations are in fine, black anaerobic clay, in proximity to much coarser sediments.

An interesting ecological observation was made while examining one specimen of *Pisidium variabile*, which has some bearing on understanding the faunal and ecological makeup of its habitat. The 1.5-mm-wide shell was found slightly gaping, with the valves still firmly attached at the hinge. Upon opening the valves, the body was absent, but inside the shell were a worm (as yet unidentified, occupying most of the internal volume of the shell), a juvenile of *Physella* sp. (the nuclear and first whorls only, lacking a body), and an unidentified orange seed to which was attached two bacterial colonies that probably were supported by a penetration of the seed coat and exudation of the nutrients (*fide* H. M. Reiswig, written commun., 1991). It appears that the worm had taken the bivalve as a refuge, capturing and consuming small organic items that passed by the gaping aperture of the shell. Whether the worm also consumed the bivalve animal, alive or dead, is not known.

Aquatic gastropods, by their feeding behavior, help improve water circulation in algal masses, and they process the ingested organic material which is reintroduced to the organic fraction of the substratum and water column; but whether they feed and process the algae themselves or the diatoms growing in them is not known. The introduction to the water column of fecal matter and other organic byproducts of animals, either naturally from indigenous fauna or artificially from human activity in the drainage, is of uncertain value to the aquatic gastropods. Aquatic gastropod faunas indigenous to spring pour-outs (for example, hydrobiids which as yet have not been reported from the Grand Canyon) also have an unknown contribution to malacofaunally centered aspects of ecology in the canyon.

Water quality is naturally of foremost importance to aquatic mollusks. Sediment load and chemical composition of the water directly affects these animals. The abundant proliferation and adaptability of some groups makes them ideal forage for fish, birds, and reptiles. For this reason the 50,000 individuals were transplanted to the fishery above Lees Ferry. Unfortunately, none of them were identified to species, and a direct comparison of species there and throughout the Grand Canyon cannot be made. Downstream transportation of individuals of successive generations is presumably a viable mechanism of species dispersal in the Colorado River corridor, but the impact that this has on native populations—as well as the impact of species mixing—in tributaries is unknown.

Only three specimens of *Fossaria* (*F. obrussa*) were collected during the 1991 reconnaissance, and these restricted to Marble Canyon. It is unclear whether they are natives or descendent from individuals possibly transplanted to the fishery above Lees Ferry.

Physella spp. are the most abundant and cosmopolitan of the Grand Canyon aquatic mollusks. Thus they are the principal topic of discussion here.

The Physidae are more tolerant of adverse ecological conditions than are some other mollusks (Burch, 1989); they can be regarded as an opportunistic group. But even though they are widespread in the region outside the Grand Canyon, it is not clear whether the Grand Canyon populations are native, or descendent from individuals transplanted to the fishery, or a cohabiting mixture of native and introduced species. As indicated in the section on identifications, specific identifications are not possible at this time

Table 7. Distribution of mollusks of the Colorado River corridor and Thunder River, Grand Canyon, collected during the 1991 reconnaissance.

Ecology: Aquatic	Ecology: Terrestrial	Taxon[1]	Lees Ferry	Vasey's Paradise	Saddle Canyon	Nankoweap Creek	Bright Angel Creek	Hermit Creek	Shinumo Creek	Elves Chasm	Blacktail Canyon	Tapeats Creek	Kanab Creek	Tuckup Canyon	Lava Falls Spring	Spring Canyon	Thunder River
		BIVALVIA															
		VENEROIDA															
		SPHAERIIDAE															
x		*Pisidium variabile* Prime, 1852	x[2]														
x		*Pisidium walkeri* Sterki, 1895	x[2]														
		GASTROPODA															
		BASOMMATOPHORA															
		LYMNAEIDAE															
x		*Fossaria obrussa* (Say, 1825)		x		x											
		PHYSIDAE															
x		*Physella* spp.	x	x		x	x	x		x	x		x	x	x		
		STYLOMMATOPHORA															
		COCHLICOPIDAE															
	x	*Cionella lubrica* (Müller, 1774)															x
		PUPILLIDAE															
	x	*Gastrocopta pellucida* (Pfeiffer, 1841)														x	

(cont'd)

Table 7 (cont'd)

Ecology: Aquatic	Ecology: Terrestrial	Taxon	Lees Ferry	Vasey's Paradise	Saddle Canyon	Nankoweap Creek	Bright Angel Creek	Hermit Creek	Shinumo Creek	Elves Chasm	Blacktail Canyon	Tapeats Creek	Kanab Creek	Tuckup Canyon	Lava Falls Spring	Spring Canyon	Thunder River
		DISCIDAE															
	x	*Discus cronkhitei* (Newcomb, 1865)															x[2]
		SUCCINEIDAE															
	x	*Catinella avara* (Say, 1824)							x								
	x	*Oxyloma* cf. *haydeni* (Binney, 1858)		x[2]													
	x	*Succinea grosvenorii* (Lea, 1864)		x	x			x				x			x		x
		ZONITIDAE															
	x	*Glyphyalinia indentata* (Say, 1823)															x
	x	*Hawaiia minuscula* (Binney, 1841)		x												x	
	x	*Zonitoides arboreus* (Say, 1817)															x[2]
		OREOHELICIDAE															
	x	*Oreohelix strigosa* (Gould, 1846)															x
		HELMINTHOGLYPTIDAE															
	x	*Sonorella coloradoensis* (Stearns, 1890)															x
		STYLOMMATOPHORA UNDET.															
	x	slugs, ?LIMACIDAE															x[2]

[1] Binomial and higher taxa follow the convention of Turgeon et al. (1988).
[2] Inside the Grand Canyon, taxon is at this time known only from this locality.

because of inadequate knowledge of anatomy and wide variation of shell morphology. We believe that the observed very wide variation in shells between all specimens collected in the Grand Canyon is an indication of multiple species in the canyon. But without specific identifications, correlation of species and habitat is not possible. In this collection, no distinct correlation has been observed between shell morphology and habitat.

Increasing amounts of sediment in the Colorado River downstream from Lees Ferry, and perhaps some chemical constraints, preclude colonization by *Physella* in the Colorado River through the Grand Canyon. Specimens that have been found there apparently have washed from the fishery above Lees Ferry or from tributaries. Individuals or dislodged egg masses may survive in the river long enough to be redeposited by currents in the mouths of wet tributaries downstream, particularly during higher river flows that inundate tributary mouths. Ebbing river flows then provide an opportunity for transplanted individuals or egg masses to be integrated with (or found) populations in those tributaries.

If downstream transport and redeposition is a viable means of dispersal in the Colorado River, it is feasible that some or all of the Grand Canyon physid populations are descendants of the individuals transplanted to the Lees Ferry fishery from the San Juan River. If this is so, dispersal through the length of the Grand Canyon could have taken place in 15 years or less since physids were reported in tributaries by Tomko (1976) and Carothers & Minckley (1981). This is an approximate distribution rate of 15-25 miles per year if the scenario of introduction is adopted. Alternatively, the reports by Tomko and by Carothers & Minckley could record native populations being slowly integrated with Lees Ferry descendents.

Physid populations probably lived in Grand Canyon tributaries in the pre-dam environment because they are so widely distributed and opportunistic in habit. Dispersal by river transport, however, would have been more hazardous in that regime because of the much heavier suspended sediment load, increasing the likelihood of suffocation. They could also have been transported into the canyon by washing down larger tributaries or by transport on aquatic birds. The latter means of dispersal, while known to occur, can be too easily cited when the mechanism of dispersal is actually unknown.

Flash floods in tributaries clearly have an impact on mollusk populations, destroying habitats as well as individuals. Complete scouring of the habitat can take place, eradicating the entire population. Three localities visited during the 1991 reconnaissance had just experienced flash floods—Hermit Creek (Mile 95.0), in the previous 24-48 hours; National Canyon (Mile 166.4), in the previous week or two; and Diamond Creek (Mile 225.7), in the previous 24 hours. The physical characteristics of each flood were different, as determined by the sediment type and distribution and damage to area vegetation. Hermit Creek was a mostly muddy water flow, as no significant fresh deposits of gravel and cobbles were seen; and large amounts of grasses were entangled around rocks and standing vegetation. Two dead snails were found in Hermit Creek. The National Canyon flood was a water flow containing gravel and cobbles; no snails were found. The Diamond Creek flood contained silt, sand, and gravel; no snails were found.

As a comparison, many habitats potentially favorable to some aquatic and terrestrial mollusks were examined in the lower ~1.0 km of Crystal Creek (Mile 98.1); but no mollusks were found. Here is an example of a creek which suffered a catastrophic debris flow, in 1966. Any snail population there was completely eradicated, as was all vegetation. If aquatic molluscan recolonization took place here, the animals may since have been overwhelmed by the dense revegetation of the tributary if not by unsuitable limnological conditions. Dense vegetation with much debris, and significant quantities of algae in the creek, may have a debilitating effect on mollusks, and perhaps the clearing effect of periodic flash floods of more normal magnitude is beneficial to the maintenance of satisfactory habitat for these animals. Alternatively, recolonization never occurred in Crystal Creek. It is of interest to note that the Crystal Creek debris fan is composed of boulders, and the mouth of the tributary is not now breached by high river flows. Floating individuals or eggs from sources upstream into the mouth of Crystal Creek find an unsatisfactory environment for survival. Significantly, we also point out that no aquatic mollusks were observed in the lower 0.5-1.0 km of Havasu Creek (Mile 156.8) during three visits (two of them non-collecting trips) by the senior author in the summer of 1991 (Table 1), while previous record of them is known at this tributary (Table 3). Havasu Creek experienced a major flash flood in September 1990, causing much physical destruction in the creek bed and removing most of the vegetation there. Havasu Creek reaches the Colorado River in a narrow defile with no emergent debris fan at its mouth; and the area experiences very heavy human use. If tributary-mouth redeposition is a viable mechanism of distribution and colonization of aquatic mollusks in the river corridor, and since Havasu Creek lacks a wide tributary mouth and pool formation in an ebbing river flow, recolonization is much more difficult. In this tributary molluscan recolonization in its lower end may take place by redistribution of individuals from favorable habitats upstream in the tributary. The permanent settlement of the Havasupai Indian Reservation, the village of Supai, is in this tributary, the waters of which also have a significant organic enrichment. The apparent absence of mollusks in the summer of 1991, so soon after the large flood, may be an indication of this mechanism of redistribution in Havasu Creek.

A second comparison of this scenario is at Bright Angel Creek (Mile 87.8). In 1966 it experienced a catastrophic flash flood from the same storm that sent a debris flow down Crystal Creek. But Bright Angel Creek had comparatively much less debris; while it, too, reformed its debris fan in the Colorado River, its mouth can be inundated by high river flows, allowing for redeposition in it of floating material from the river.

During the 1991 reconnaissance, no definite correlation was noted between physical/vegetational conditions in tributaries and the abundance (or even presence) of aquatic gastropods. Predictive methods, based on observations made during the earlier part of the river trip, did not always hold true. Where some tributaries seemed to host physical conditions ideally suited to aquatic gastropods, no animals were seen. Either the populations live further upstream along these tributaries, or particular limnological constraints preclude their survivability there. While there are reports available on tributary water quality in the Grand Canyon (e.g., Cole & Kubly, 1976; Sommerfeld et al., 1976), the conditions were not measured at the time mollusk collection sites were examined during the present survey. In some instances, molluscan communities may have been decimated by recent flash floods; if still present in these tributaries they may be in few enough numbers and widely spaced populations to have eluded detection during the short time collectors were on site. Calcium, in the form of calcium carbonate ($CaCO_3$), is necessary for the production of shell material, but no direct correlation was observed between the $CaCO_3$ content of tributary waters to the abundance of aquatic mollusks. The wet tributaries often are rich in magnesium, too, in the form $(Ca,Mg)CO_3$ originating in groundwater of more dolomitic rock strata, but to the aquatic gastropods the benefits or disadvantages of this element in the carbonate is unknown.

Specific habitat types where aquatic gastropods occurred in the Grand Canyon varied. Most habitats were silt- and algae-lined pools with standing or very slowly moving water. In other places, gastropods were found alongside swiftly running currents, either at the edge of the current or in the shelter of rocks and vegetational debris. Some gastropods even attached themselves to the downcurrent sides of vegetation or rocks in all but the swiftest currents. They were more active in calmer pools, leaving grazing trails in the fine silt and algae. Pools that were heavily lined or clogged with algae did not contain gastropods. It is not clear whether diatoms attached to the algal films and strands are a food source for the aquatic gastropods. Some diatoms of the Colorado River and its tributaries show characteristic preferences for specific chemical conditions (Czarnecki & Blinn, 1978), as apparently so do some of the gastropods. Studies of correlative relationships between these organisms might help toward understanding the distribution of the gastropods.

Bright Angel Creek is a somewhat anomalous molluscan habitat when its physical characteristics are considered. Water current in the reach between the river and Phantom Ranch is relatively swift, and gastropods are found abundantly along the sides of the stream. Alongside Bright Angel Campground, the streambanks have been rip-rapped to control erosion in this heavily used area. The gastropods in lower Bright Angel Creek are attached to everything, without regard to water current velocity (except in the swiftest currents), protection, or silt/algae bottom covering; they are found on the bottom, on rocks, on living and dead vegetation, both in and out of the water. The heavy human use of the area may be a contributing factor in the proliferation of physids in this stream. A heavily used campground, bunkhouses, and mule corral are near the creek; moderately heavy use of the entire creek to its source is enjoyed by hikers; and there is a permanent household near its source (the waterline pumphouse attendant's family). All these activities provide enrichment which the physids find very favorable. The calcium carbonate fraction of the water appears to be beneficial to these organisms; its source is the magnesium-calcium carbonate terrain of the Kaibab Plateau (in the Kaibab and Toroweap rock formations that form the plateau cap.

In contrast, Havasu Creek is a permineralized stream which has its source in magnesium-calcium carbonate terrain of the Coconino Plateau (also capped by the Kaibab and Toroweap formations) and which also has organic enrichment from the village of Supai and from campgrounds in the national park nearer the river. Havasu Creek should be host to many aquatic mollusks, but their apparent absence in the lower end of the tributary, as noted above, may be due to the effects of the flash flood of 1990.

Physids were seen abundantly also at Elves Chasm (Mile 116.6). The stream course there is mostly a chute-and-pool configuration, with water running swiftly over large exposures of bedrock. Algae coat the edges of the chutes, and silt and algae line some of the pools. Physids were found both alongside the chutes and in many of the pools, particularly at the plunge pool beneath the waterfall where they were found attached to the walls above and beneath the water surface (but avoiding the darkest and mossy areas). This is another heavy human-use area. The stream drains from the magnesium-calcium carbonate terrain of the Coconino Plateau, but in addition there are large deposits of travertine (calcium carbonate) at Elves Chasm, dissolution of some of which by rainfall may contribute to the carbonate fraction of the water.

Large numbers of physids were also taken at Vasey's Paradise (another magnesium-calcium carbonate-rich water source) and at Lava Falls Spring. The latter site is different in that it is a warm spring issuing from a carbonate-rich rock formation, the Muav Limestone. Physids were seen in great abundance, but mortality among them was very high; most were dead. Furthermore, the water chemistry there is such that the dead shells are bleached and partly dissolved so that they are thin and malleable. It is unclear whether the high mortality was due to the water chemistry and temperature, or whether the site was visited at a critical point of the population's life cycle.

The comparatively large number of physids collected at Kanab Creek (Mile 143.4) are indirectly an indication of favorable habitat in this drainage, although the point of collection was in a single silt-lined pool in a gravel and cobble bar exposed to direct sunlight. Kanab Creek is a significant regional drainage, with a geomorphologically mature grade indicating greater age than for other tributaries in the area. Its waters have been reported to have a high magnesium content (Sommerfeld et al., 1976). When the site was visited in early August 1991, the creek emerged from its bed of sand, gravel, and cobbles only near its mouth, where it soon mixed with the colder water of the Colorado River. One 1-m-deep pool was found <0.5 km from the mouth of the creek, containing hundreds of fully mature physids. No other pools, wet or dry, were seen in this 0.5-km reach.

The Colorado River probably distributes aquatic mollusks between tributaries. The limnological characteristics of the river, particularly sediments and nutrients, are unsatisfactory below Lees Ferry for the rapid introduction and support of many aquatic invertebrates to the river, including mollusks. Thus in the context of mainstream biomass the river acts as a faunal barrier to mollusks, a concept long recognized (e.g., Bartsch, 1916; Goodrich, 1921). More resilient species such as the Physidae appear to tolerate adverse conditions in the river for long enough to reach the safe haven of wet tributaries, although the ratio of successfully and unsuccessfully redeposited individuals and eggs is unknown. Individuals of breeding age are known also to have egg masses attached to their shells (Baker, 1911; and specimens of ***Physella*** sp. so observed at Vasey's Paradise), so such specimens washed to the river and redeposited in other tributaries serve doubly in this mechanism of dispersal.

The rapids of the Colorado River have an unknown impact on molluscan distribution in the Colorado River. They are effecuve barriers to upstream communication of species, particularly in the view that the aquatic species that have been recorded from the river corridor are not parasitic on, nor have larval stages dependent upon, fishes; this includes the bivalves (sphaeriids) seen in the fishery at Lees Ferry (for a comparative example of the concept, see Jenkinson, 1974). The mortality rate of aquatic gastropods in passage through rapids is unknown.

Terrestrial Mollusks

The habitats of terrestrial gastropods are in proximity to water even if they do not require a water source as such; some live under rocks, feeding on vegetational debris or fungus. They do require rocks or vegetational litter also for shelter from dehydration and predators. A few forms, such as ***Oreohelix***, are calciphiles and can be found hidden deep in limestone talus or attached to secluded limestone walls or in soils derived from limestone outcrops. It is reasonable to expect that in the controlled river environment today, protected from large seasonal floods, terrestrial mollusks would find more favorable habitats along the Colorado River. But with the notable exception of Vasey's Paradise, and a few specimens taken at Lava Falls Spring, there is no current evidence of terrestrial gastropods alongside the river above the high water zone; when they were found in the river corridor it was in the area of tributary mouths. Even dead (empty) shells are an indication of the presence of populations, but none were found along the river during the 1991 reconnaissance.

Terrestrial gastropods such as succineids live in a setting of emergent vegetation and litter. Groups that harvest living vegetational tissue inhabit areas that host sufficient plant growth, in moist and wet areas; in the Grand Canyon this is exclusively in the presence of perennial water. The processing of decaying organic matter by other gastropod groups such as zonitids is an activity of unknown significance in the Grand Canyon ecosystem. While dead vegetation abounds, water supplies are scarce; the degree of correlation necessary to support such molluscan communities there is not known. Calciphilous terrestrial gastropods like the oreohelicids could proliferate in limestone locales throughout the Grand Canyon. Pilsbry & Ferriss' (1911) report (and examination of their collections in the Academy of Natural Sciences of Philadelphia) shows that huge colonies can exist under appropriate conditions of (but not necessarily requiring all) limestone talus, protection from dehydration, and occasional availability of water either from a ground source or from precipitation. The numbers seen at Thunder River corroborate this view.

The methods of distribution of terrestrial gastropods are not well documented. More than a few individuals are usually required to establish successful colonies, although gravid adults can feasibly found a new colony after transport. The mechanisms of transport can vary, but wind plays an important role in dispersal, particularly of the smallest terrestrial gastropods; this mechanism is especially significant in the arid Southwest (Bequaert & Miller, 1973). In the canyons, gravity also is a likely mechanism of dispersal.

At Vasey's Paradise, three species of terrestrial gastropods were found, all requiring proximity to water—two species of Succineidae, and one species of Zonitidae (see Table 7). The zonitid, *Hawaiia minuscula* (Binney, 1841), was found only dead in a pool at the bottom of the cliff; they may have fallen in from adjacent vegetated steep slopes if not from above. One of the succineids is a species of *Oxyloma*, whose generic identification was confirmed on the basis of anatomy of the genitalia. It is the first record of the genus alive in Arizona, previously known in the state by fossils (Bequaert & Miller, 1973; Mead, 1991). Specific identification is referred to *O. haydeni* (Binney, 1858) based on the genitalia; however, the observed characters do not wholly agree with illustrations of the genitalia of *O. haydeni*. It does not appear to be the similar *O. retusa* (Lea, 1834), and it feasibly could be a new species; at the time of this writing, further anatomical studies are being arranged. Vasey's Paradise has long been recognized as a remarkable biotic community, and the molluscan fauna there corroborates this statement. It hosts at least five species of mollusk (of four families), including thusfar the only known living colony of *Oxyloma* in Arizona.

Succineid species, at least, have been in the Colorado River corridor of Grand Canyon for some time. Fossil or subfossil shells referred to *Succinea grosvenorii* (Lea, 1864) were found in red earth along the trail at Saddle Canyon (Mile 47.0). They were lodged in accumulated silt between blocks that fill an ill-defined drainage that is a minor tributary ending at the mouth of Saddle Canyon. Sheltered surfaces of the surrounding rocks were covered with small amounts of dead moss-like vegetation. The immediate vicinity is exposed and receives direct sunlight, making this part of the trail very hot in summer. Whatever water source existed here is no longer present, and the biotic community has died. No obvious source was seen from the trail. Considering the long term of survival of paleontological remains in the semiarid environment of the inner canyon (e.g., Cole, 1985), the succineid shells at Saddle Canyon could be very old (hundreds to thousands of years). We do not provide conjecture on their actual age in the absence of absolute dating by radiometric techniques. We see them of significant age and as evidence of non-physid mollusks living in the Colorado River corridor long before the appearance of Glen Canyon Dam. The shell carbonate δO^{18} values may provide information on atmospheric water vapor at the site when the animals were alive, providing a paleontological example of molluscan living environments along the Colorado River. (It is of further interest to point out that the living mollusks collected along the creek in Saddle Canyon are also referred to *S. grosvenorii*.)

Other records of fossil mollusks in the Grand Canyon are from areas away from the Colorado River corridor, but they, too, were found in silty red earth. These were described as new oreohelicid subspecies *Oreohelix yavapai fortis* Cockerell, 1927 (= *O. yavapai* Pilsbry, 1905), found along Bright Angel Trail, and *O. y. vauxae* Marshall, 1929 (= *O. yavapai*), at Supai, Havasu Canyon.

Other than Vasey's Paradise, the only other significant population of terrestrial gastropods seen in the Colorado River corridor during the 1991 reconnaissance was at Spring Canyon (Mile 204.3). At the closest possible approach to the spring pour-out hidden in impassable vegetation, many dead specimens of *Hawaiia minuscula* were found in mud beneath the pour-out area. Some specimens taken from entangled roots not directly in the water may have been living. The geographic separation of *H. minuscula* taken here and at Vasey's Paradise may be a statistical artifact of non-collection. The species is probably more widely distributed in the river corridor, but its tiny size and secretive habits make it difficult to find.

The survey made at Thunder River, although not in the Colorado River corridor, is a representative look at the potential for species abundance in a riparian community in the Grand Canyon. As noted later in this report, several species occur there at lower elevations than those in which they normally occur; this is due to exceptionally favorable ecological conditions. In one hour of collecting, eight species were obtained (in seven families), including the first record of slugs (?Limacidae) inside the Grand Canyon.

INFLUENCE OF THE COLORADO RIVER

The fluctuations of the flow of the Colorado River regularly inundates shorelines and tributary mouths. Aquatic mollusks of the lowest reaches of tributaries, within the fluctuation zone, are clearly affected by these floods. Terrestrial gastropods that live above the high-water zone are affected indirectly by alterations of vegetational and sedimentological conditions caused by changes to the river flow regime.

Questions posed about the direct effects of changing flows from Glen Canyon Dam on the molluscan fauna of the river corridor are unresolved because of the lack of previous data. Earlier river surveys cursorily included aquatic mollusks in their field observations but did not mention the animals in their conclusions, except under the general term "aquatic resources"; terrestrial mollusks have been virtually ignored. All mollusks should be included in the monitoring process since many are easily found and collected, and they are one food resource of some fish and terrestrial vertebrates.

Aquatic Mollusks

Most aquatic mollusks require complete immersion and do not aestivate if stranded by ebbing waters; others survive out of water for periods of time, living amphibiously around the water-air interface. They can also raft at the air-water interface, floating upsidedown in pools or in currents (although none were so observed during the 1991 reconnaissance). Mollusk populations that live in the mouths of wet tributaries are susceptible to frequent deep immersion in colder river water that is increasingly more sediment-laden downstream through the Grand Canyon. In the process, they can be swept into the river by themselves or attached to vegetation, where they die if they are not redeposited in another suitable habitat; specifically, other tributary mouths. The cold water probably is not a direct factor in mollusk mortality since they live in the cold river between Glen Canyon Dam and Lees Ferry. But the often daily immersion in cold water, alternating with exposure to warmer tributary flows and stranding in solar-heated pools left by ebbing river flows, is a factor of unknown impact to survival and productivity.

A potentially negative impact of fluctuating river flows, particularly on a daily basis, is on the redistribution of individuals and egg masses. High flows can remove individuals and eggs from tributary mouths and redeposit them in other tributaries downstream. In the flow regime of an uncontrolled river, redeposited individuals will likely survive to reach levels in the tributary that are above flood flow levels; redeposited egg masses will likewise have a chance to survive to their full term of development before the next flood occurrence. By that time, particularly if a seasonal flow was responsible for the initial redeposition, the survivors will be fully integrated with the existing population of the tributary. However, in a river regime with daily or other frequent fluctuations, rather than one-time random or seasonal ones, once-transplanted individuals or eggs may be taken again into the river, with fatal consequences if they are not fortunately redeposited again in another tributary.

Productivity of aquatic mollusks of the Colorado River corridor is unmeasured. There is potential for significant productivity in each wet tributary. Seasonal aspects of productivity in the Grand Canyon are unknown. Variable river flows will continue to transport individuals and eggs to new habitats at a rate that is more frequent than by naturally varying (seasonal) flows. The intermixing rate between populations is increased if levels of successful redeposition do not exceed the levels of washout by the action of tributary runoff and by the inundation of the next rise in river level. The frequencies of washout and redeposition are unknown. Just how this increased rate of transportation and population mixing affects the trophic aspects of the malacofauna likewise is unknown. The limitations on colony sizes are not known for the inner canyon, and the relationship between colony sizes and their use as food by aquatic and terrestrial organisms remains to be determined.

An empirical example of distribution of mollusks by the Colorado River may have been observed during the 1991 reconnaissance. Nankoweap Creek (Mile 52.1) was searched for about 2 km from its mouth. Although many habitats seemed to be physically favorable to aquatic mollusks, they were not seen. Physical evidence of recently ebbing water level was observed along the creek. But only in the 100 m or so nearest the river were there aquatic gastropods, mostly physids. At the time of visitation, the river level was ebbing, leaving pools along the outer parts of the sediment fan at the creek mouth. The gastropods were found in the creek and in one of the pools which at the time of collection still had direct communication with the river. Another collector also obtained a few snails from the edge of the river about 150 m upstream from the mouth of Nankoweap Creek. Nowhere else below Lees Ferry during the 1991 reconnaissance were mollusks found in the river or in pools left by ebbing river flows (except for a single specimen at Vasey's Paradise which had obviously just washed into the river). The Nankoweap Creek population may be a transitional one, perhaps recolonizing an area scoured out by a flash flood.

Gastropods that are left stranded in pools are susceptible to predation and mortality due to unfavorable changes of pool conditions. Summertime exposure of these pools can raise the water temperatures to levels lethal to the gastropods. If this is repeated daily, there is a negative impact on the population, one which would not otherwise occur along an uncontrolled river. Drying of pools, too, is of obvious consequence to stranded gastropods. None were observed in the 1991 reconnaissance, but at Elves Chasm a stranded community of physids in a dried pool along Royal Arch Creek was taken as a comparative sample.

Aquatic mollusks living in wet tributaries beyond the reach of high river flows are not directly affected by fluctuating river levels. They could be influenced to some extent by changes to the riparian community, as instigated by changes to the flow regime of the river, including those effects that influence the distribution and foraging activities of predators. Mollusks living even further upstream in these tributaries should not be affected at all by changing river regimes. Their cycles of productivity are probably those that have always existed in the tributaries, influenced only by limnological factors of the creek and the periodic impact of flash floods.

Complete eradication of populations by debris flows sets the stage for recolonization by whatever means of distribution are successful. If recolonization is effected from transplanted river-borne living individuals or egg masses, access to the streamcourse above the level of high river water must be had before successful recolonization is expected. This requires either that the debris fan be reasonably diffuse, allowing immersion of suitable habitats, or that a new access channel be cut through it by normal tributary runoff or by another flood.

Terrestrial Mollusks

By definition, terrestrial gastropods do not tolerate immersion, thus they will not live at any normal river level. For this reason, the stable riverside vegetational communities that have developed along the Colorado River since 1963 might be candidate sites for colonization by terrestrial gastropods. Aside from the community at Vasey's Paradise, however, no evidence of terrestrial mollusks was seen in or above the high water zone during the 1991 reconnaissance. Dead shells were sought as indicators of the presence of terrestrial mollusks, but despite the availability of vegetational debris, shelter, and moisture (or limestone talus for calciphilous species), none were found during the brief examinations.

Where terrestrial gastropods were found in areas in communication with the river corridor, they were so placed that they could not be affected by high river flows. Only through the indirect effects of moderating vegetational communities and activity of foragers are the terrestrial species influenced by changing river regimes.

The Thunder River fauna is an indication of the potential diversity for terrestrial gastropods in a Grand Canyon riparian setting, outside of which is inhospitable. It is also an example of a habitat for species out of their normal range of elevation, a significant factor in the distribution of terrestrial gastropods. The vegetational and faunal communities at Thunder River are unaffected by inundation and are, through natural dispersal mechanisms, in communication with both the semiarid canyon interior and the temperate Kaibab Plateau. Malacologically, the Thunder River community is composed of species of from different life zones; it contains terrestrial species more representative of the canyon interior (*Succinea grosvenorii*, *Sonorella coloradoensis*) and species more representative of the Kaibab Plateau (slugs, here identified as ?Limacidae; *Oreohelix strigosa*, *Zonitoides arboreus*, *Discus cronkhitei*, and *Cionella lubrica*).

BIOGEOGRAPHY

Previous publications provide some insight on the occurrences of molluscan taxa in the Grand Canyon region (Table 8, and Bequaert & Miller, 1973). Most species occurring in the area are not important to understanding molluscan biogeography, but the aspect of biogeography of terrestrial mollusks includes the third dimension of altitude as reflected in biological life zones.

Most of the mollusks found during the 1991 reconnaissance between Lees Ferry and Diamond Creek are known to live in the Grand Canyon region (see Bequaert & Miller, 1973). Ten species, however, are new records for the Grand Canyon (Table 9). Of these, three are new records for the region (the Grand Canyon vicinity and southernmost Utah, within the limits of the Southwestern Molluscan Province), and two are new records for the state of Arizona.

Based on previous publications of molluscan occurrences in the Grand Canyon region, and on new data presented in this report, we have compiled a working list of Mollusca of northwestern Arizona (Table 10). These taxa may occur in the Grand Canyon, including the river corridor. Some distributional notes, as molluscan biogeographical elements, are worth mentioning.

Sphaeriidae

Pisidium variabile Prime, 1852, is a cosmopolitan species in the United States and Canada (Burch, 1975), but record of it in Arizona has apparently been lacking since it is omitted by Bequaert & Miller (1973). Its occurrence in Arizona is verified here. *P. walkeri* Sterki, 1895, is previously recorded in Arizona (Bequaert & Miller, 1973; Mead, 1991), although not in the Grand Canyon region.

Succineidae

Oxyloma cf. *haydeni* has been found at Vasey's Paradise. The genus is distributed widely; still it has not been reported living (but only as fossils) in Arizona (Bequaert & Miller, 1973; Mead, 1991). Anatomical dissection of the body confirms its identity as *Oxyloma*, with indications that it may be the species *O. haydeni* (Binney, 1858); it does not appear to be the similar *O. retusa* (Lea, 1834) of the northern United States and Canada. *O. haydeni*, as its synonymous taxon *O. h. kanabensis* Pilsbry, 1948, is reported from Kanab Creek six miles north of Kanab, Utah, and *O. haydeni* is known from the greater northwestern United States

Table 8. Distribution of mollusks of the Grand Canyon and adjacent plateaus reported in previous literature other than surveys of the Colorado River[1]

Taxon (as published, new species-level taxa indicated by **bold face**; synonymy added)	Localities (**bold face** indicates direct communication with Colorado River corridor)[2]
STEARNS (1890)	
HELMINTHOGLYPTIDAE	
Helix (*Arionta*) ***coloradoensis*** **Stearns, 1890** [= *Sonorella coloradoensis* (Stearns)]	Near Hance Trail
PILSBRY & FERRISS (1911)	
BIVALVIA	
SPHAERIIDAE	
Pisidum sp. undet.	The Greens, Kanab Creek, near Kanab, Utah
GASTROPODA	
LYMNAEIDAE	
Lymnaea parva Lea, 1841 [= *Fossaria parva*]	Pipe Spring
Lymnaea obrussa Say, 1825 [= *Fossaria obrussa*]	Deception Lake, near Kanab, Utah
PHYSIDAE	
Physa gyrina Say, 1821 [= *Physella gyrina*]	The Greens, Kanab Creek, Kanab, Utah
Physa humerosa Gould, 1855 [= *Physella humerosa*]	Indian Gardens
Physa virgata Gould, 1855 [= *Physella virgata*]	Pipe Spring
PLANORBIDAE	
Planorbis deflectus Say *in* Keating, 1824[3] [= *Gyraulus deflectus*]	Fredonia
COCHLICOPIDAE	
Cochlicopa lubrica (Müller, 1774) [= *Cionella lubrica* (Müller)]	Bright Angel Trail Indian Gardens Bass Trail
PUPILLIDAE	
Bifidaria pellucida hordeacella (Pilsbry, 1890) [= *Gastrocopta pellucida* (Pfeiffer, 1841)]	Bass Trail

Table 8 (cont'd)

Taxon (as published, new species-level taxa indicated by **bold face**; synonymy added)	Localities (**bold face** indicates direct communication with Colorado River corridor)[2]
PILSBRY & FERRISS, 1911 (CONT'D)	
SUCCINEIDAE	
Succinea avara Say, 1824 [= *Catinella avara*]	Bass Station Bass Trail **Shinumo Creek** White Creek Muav Saddle Kaibab Plateau Mt. Trumbull
Succinea retusa Lea, 1834 [= *Oxyloma retusa*]	The Greens, Kanab Creek, Kanab, Utah
Succinea hawkinsi Baird, 1863 [= *Oxyloma hawkinsi*]	The Greens, Kanab Creek, Kanab, Utah
Succinea grosvenorii Lea, 1864	Kaibab Plateau Antelope Valley Mt. Trumbull
HELICARIONIDAE	
Euconulus fulvus alaskensis (Pilsbry) [= *Euconulus fulvus* (Müller, 1774)]	Bright Angel Trail Bass Trail Powell Plateau Kaibab Plateau Mt. Trumbull
ZONITIDAE	
Zonitoides minuscula (Binney, 1841) [= *Hawaiia minuscula*]	Mt. Trumbull
Zonitoides arboreus (Say, 1817)	Kaibab Plateau
Vitrea indentata umbilicata Cockerell, 1899 [= *Glyphyalinia indentata* (Say, 1823)]	Bright Angel Trail Bass Station Mojave Amphitheater Powell Plateau Kaibab Plateau
VITRINIDAE	
Vitrina alaskana Dall, 1905	Bass Trail Kaibab Plateau
LIMACIDAE	
Agriolimax hemphilli ashmuni Pilsbry & Vanatta *in* Pilsbry & Ferriss, 1910 [= *Deroceras laeve* (Müller, 1774)]	Kaibab Plateau
THYSANOPHORIDAE	
Thysanophora ingersolli (Bland, 1875) [= *Microphysula ingersollii*]	Kaibab Plateau Muav Saddle
Thysanophora hornii (Gabb, 1866)	**Shinumo Creek**

Table 8 (cont'd)

Taxon (as published, new species-level taxa indicated by **bold face**; synonymy added)	Localities (**bold face** indicates direct communication with Colorado River corridor)[2]
PILSBRY & FERRISS, 1911 (CONT'D)	
Bifidaria pilsbryana Sterki, 1890 [= *Gastrocopta pilsbryana*]	Bright Angel Trail Bass Trail Muav Saddle Kaibab Plateau Mt. Trumbull
Bifidaria ashmuni Sterki, 1898 [= *Gastrocopta ashmuni*]	Bright Angel Trail Muav Saddle Kaibab Plateau Mt. Trumbull
Pupoides marginata (Say, 1821) [*Pupoides albilabris* (C.B. Adams, 1841, *nom. nov.*)] [= *Pupoides nitidulus* (Pfeiffer, 1859)]	Mt. Trumbull
Pupoides hordacea (Gabb, 1866)	Mt. Trumbull Antelope Valley
Pupoides syngenes (Pilsbry, 1890) [= *Pupilla syngenes*]	Bright Angel Trail Bass Trail Powell Plateau Muav Saddle Kaibab Plateau
Pupilla syngenes form *dextroversa* (Pilsbry & Vanatta, 1900) [= *Pupilla syngenes* (Pilsbry, 1890)]	Bass Trail Kaibab Plateau
***Pupilla syngenes avus* Pilsbry & Ferriss, 1911** [= *Pupilla syngenes* (Pilsbry, 1890)]	Bass Trail
***Pupilla hebes kaibabensis* Pilsbry & Ferriss, 1911** [= *Pupilla hebes* (Ancey, 1881)]	Muav Saddle
VALLONIIDAE	
Vallonia cyclophorella "Ancey" Sterki, 1892	Bright Angel Trail Indian Gardens Muav Saddle Kaibab Plateau Mt. Trumbull
Vallonia perspectiva Sterki, 1893	Bass Trail
DISCIDAE	
Pyramdula (Gonyodiscus) cronkhitei (Newcomb, 1865) [= *Discus cronkhitei*]	Kaibab Plateau Mt. Trumbull Kanab, Utah

Table 8 (cont'd)

Taxon (as published, new species-level taxa indicated by **bold face**; synonymy added)	Localities (**bold face** indicates direct communication with Colorado River corridor)[2]
PILSBRY & FERRISS, 1911 (CONT'D)	
OREOHELICIDAE	
***Oreohelix yavapai profundorum* Pilsbry & Ferris, 1911** [= *O. yavapai* Pilsbry, 1905]	Bass Trail
***Oreohelix yavapai extremitatis* Pilsbry & Ferris, 1911** [= *O. yavapai* Pilsbry, 1905]	Bass Trail
***Oreohelix yavapai angelica* Pilsbry & Ferriss, 1911** [= *O. yavapai* Pilsbry, 1905]	Bright Angel Trail
Oreohelix strigosa depressa (Cockerell, 1890)[4] [= *O. strigosa* (Gould, 1846)]	Kaibab Plateau Shinumo Canyon, head Muav Saddle Powell Plateau
HELMINTHOGLYPTIDAE	
Sonorella coloradoensis (Stearns, 1890)	Bass Station Bright Angel Trail Bass Trail **Shinumo Creek** White Creek Mojave Amphitheater Powell Plateau Muav Saddle
HENDERSON (1914)	
HELMINTHOGLYPTIDAE	
***Sonorella betheli* Henderson, 1914**[5] [= *Helminthoglypta traski* (Newcomb, 1861)	Bright Angel Trail[5]
COCKERELL (1927)	
OREOHELICIDAE	
***Oreohelix yavapai fortis* Cockerell, 1927** [fossil or subfossil] [= *O. yavapai* Pilsbry, 1905]	Bright Angel Trail
MARSHALL (1929)	
OREOHELICIDAE	
***Oreohelix yavapai vauxae* Marshall, 1929** [fossil or subfossil] [= *O. yavapai* Pilsbry, 1905]	Supai, Havasu Canyon
MILLER (1984)	
HELMINTHOGLYPTIDAE	
***Sonorella reederi* Miller, 1984**	**Just west of Rampart Cave**

Notes to Table 8

[1] This list summarizes the previous understanding of the diversity and distribution of mollusks of the Grand Canyon and adjacent plateaus. It includes the area north of the Grand Canyon to the boundary of the Southwestern Molluscan Province (see Bequaert & Miller, 1973). Note that little has been reported from areas that can be interpreted to be in direct communication with the Colorado River corridor. References are cited in chronological order. Synonyms are listed to provide more recent nomenclature for these names. Higher taxa and synonyms are as given in Turgeon et al. (1988).

[2] Precise localities itemized by authors are grouped here by general area; for example, all Kaibab Plateau localities are listed only as "Kaibab Plateau."

[3] Specimens of *Planorbis deflectus* (= *Gyraulus deflectus*) reported by Pilsbry & Ferriss (1911) from Fredonia, Arizona, are in ANSP collection as *Gyraulus parvus* (Say, 1817). Bequaert & Miller (1973) indicate that *G. deflectus* is known only as fossils in Arizona.

[4] Bequaert & Miller (1973:126) note that the nominate *Oreohelix strigosa strigosa* (Gould) occurs neither in Arizona nor in the Southwestern Molluscan Province. The Grand Canyon forms have been identified as *O. s. depressa* (Cockerell), although certain identification of specimens included in the present report are to the species *O. strigosa* (Gould) only, based on anatomy (*teste* K.C. Emberton).

[5] Pilsbry (1939:172) indicated that the locality is in error, that the types of *Sonorella betheli* were probably from near Los Angeles, California. Pilsbry placed the species in synonymy with *Helminthoglypta traski.*

Table 9. New records of occurrence of mollusks in the Grand Canyon and vicinity.[1]

	AZ	R	GC
BIVALVIA			
SPHAERIIDAE			
Pisidium variabile Prime, 1852	x	x	x
Pisidium walkeri Sterki, 1895		x	x
GASTROPODA			
LYMNAEIDAE			
Fossaria obrussa (Say, 1825)		x	x
PUPILLIDAE			
Gastrocopta pellucida (Pfeiffer, 1841)			x
DISCIDAE			
Discus cronkhitei (Newcomb, 1865)			x
SUCCINEIDAE			
Succinea grosvenorii Lea, 1864			x
Oxyloma cf. *haydeni* (Binney, 1858)	x		x
ZONITIDAE			
Hawaiia minuscula (Binney, 1841)			x
Zonitoides arboreus (Say, 1817)			x
STYLOMMATOPHORA undet.			
slugs, ?LIMACIDAE			x

[1] New records of occurrence: AZ = Arizona, R = regional (Grand Canyon vicinity, northwestern Arizona and adjacent southernmost Utah, within the Southwestern Molluscan Province), GC = Grand Canyon (including Marble Canyon). Higher taxa and binomens follow the convention of Turgeon et al. (1988).

Table 10. Working list of Mollusca of northwestern Arizona (assembled from published literature and field surveys for the present report).[1]

Taxon (bold face indicates taxon is reported from the Grand Canyon, including taxa reported herein for the first time)	**Identifications of Bequaert & Miller (1973)**
BIVALVIA	
SPHAERIACEA	
SPHAERIIDAE	
***Pisidium variabile* Prime, 1852**	Not listed
***Pisidium walkeri* Sterki, 1895**	*Pisidium walkeri* Sterki, 1895
GASTROPODA	
LYMNAEACEA	
LYMNAEIDAE	
***Fossaria obrussa* (Say, 1825)**	*Fossaria obrussa* (Say, 1825)
***Fossaria parva* (Lea, 1841)**	*Fossaria parva* (Lea, 1841)
Fossaria techella (Haldeman, 1867)	*Stagnicola (Bakerilymnaea) bulimoides techella* (Haldeman)
ANCYLACEA	
PHYSIDAE[2]	
Physella gyrina (Say, 1821)	[Mentioned in discussion on p. 202.]
Physella squalida (Morelet, 1851)	Not listed
Physella virgata (Gould, 1855)	*Physa (Physella) virgata virgata* Gould, 1855
Physella humerosa (Gould, 1855)	*Physa (Physella) humerosa* Gould, 1855
Physella osculans (Haldeman, 1843)	Not listed
Physella propinqua (Tryon, 1865)	Not listed
PLANORBIDAE	
Gyraulus deflectus (Say *in* Keating, 1824)	Known only as fossils in Arizona
Gyraulus parvus (Say, 1817)	*Gyraulus (Torquis) parvus* (Say, 1817)
Planorbella tenuis ("Philippi" Dunker, 1850)	*Helisoma (Pierosoma) tenue* (Dunker, 1850)
Planorbella trivolvis (Say, 1817)	Authors indicate that some identifications of *H. trivolvis* may be *H. tenue*, possibly also that the two are synonyms
ANCYLIDAE	
Ferrissia parallela (Haldeman, 1841)	*Laevipex parallela* (Haldeman, 1841) [fossil only]
CIONELLACEA	
COCHLICOPIDAE	
***Cionella lubrica* (Müller, 1774)**	*Cochlicopa lubrica* (Müller, 1774)

Table 10 (cont'd)

Taxon (bold face indicates taxon is reported from the Grand Canyon, including taxa reported herein for the first time)	Identifications of Bequaert & Miller (1973)
PUPILLACEA	
PUPILLIDAE	VERTIGINIDAE
Vertigo concinnula Cockerell, 1897	*Vertigo* (*Vertigo*) *modesta insculpta* Pilsbry, 1919
Vertigo gouldii (Binney, 1843)	*Vertigo* (*Vertigo*) *gouldii* (Binney, 1843) With the following varieties: *coloradensis* (Cockerell, 1891) *arizonensis* Pilsbry & Vanatta, 1900 *inserta* Pilsbry, 1919
	PUPILLIDAE
Gastrocopta ashmuni (Sterki, 1898)	*Gastrocopta* (*Immersidens*) *ashmuni* (Sterki, 1898)
***Gastrocopta pellucida* (Pfeiffer, 1841)**	*Gastrocopta* (*Gastrocopta*) *pellucida* (Pfeiffer, 1841)
Gastrocopta quadridens Pilsbry, 1916	*Gastrocopta* (*Staurotrema*) *quadridens* Pilsbry, 1916
Gastrocopta pilsbryana (Sterki, 1890)	*Gastrocopta* (*Vertigopsis*) *pilsbryana* (Sterki, 1890) Also with the variety *ammisidens* Pilsbry, 1934, placed in synonymy
Gastrocopta pentodon (Say, 1822)	*Gastrocopta* (*Vertigopsis*) *pentodon* (Say, 1822)
Gastrocopta holzingeri (Sterki, 1889)	Not listed
Pupilla hebes (Ancey, 1881)	*Pupilla hebes* (Ancey, 1881) Also with the variety *kaibabensis* Pilsbry & Ferriss, 1911, placed in synonymy
Pupilla muscorum (Linné, 1758)	*Pupilla muscorum* (Linné, 1758)
Pupilla syngenes (Pilsbry, 1890)	*Pupilla syngenes* (Pilsbry, 1890) Also with the following varieties placed in synonymy: *avus* Pilsbry & Ferriss, 1911 *dextroversa* Pilsbry & Vannata, 1900
Pupoides albilabris ("Ward" C.B. Adams, 1841)	*Pupoides* (*Pupoides*) *albilabris* (C.B. Adams, 1841)
Pupoides hordaceus (Gabb, 1866)	*Pupoides* (*Ischnopupoides*) *hordaceus* (Gabb, 1866)
VALLONIIDAE	
Vallonia cyclophorella "Ancey" Sterki, 1892	*Vallonia cyclophorella* Sterki, 1892
Vallonia perspectiva Sterki, 1893	*Vallonia perspectiva* Sterki, 1893
ARIONACEA	
CHAROPIDAE	ENDODONTIDAE
Radiodiscus millecostatus Pilsbry & Ferriss, 1906	*Radiodiscus millecostatus* Pilsbry & Ferriss, 1906
DISCIDAE	ENDODONTIDAE
***Discus cronkhitei* (Newcomb, 1865)**	*Discus* (*Discus*) *cronkhitei* (Newcomb, 1865)

Table 10 (cont'd)

Taxon (**bold face** indicates taxon is reported from the Grand Canyon, including taxa reported herein for the first time)	**Identifications of Bequaert & Miller (1973)**
SUCCINACEA	
SUCCINEIDAE	
***Catinella avara* (Say, 1824)**	*Succinea* (*Novisuccinea*) *avara* Say, 1824
Oxyloma hawkinsi (Baird, 1863)	Not listed
***Oxyloma* cf. *haydeni* (Binney, 1858)**	Not listed
Oxyloma retusa (Lea, 1834)	Not listed
***Succinea grosvenorii* Lea, 1864**	*Succinea* (*Novisuccinea*) *grosvenorii* Lea, 1864
ARIOPHANTACEA	
HELICARIONIDAE	EUCONULIDAE
Euconulus fulvus (Müller, 1774)	*Euconulus fulvus* (Müller, 1774)
ZONITACEA	
ZONITIDAE	
Glyphyalinia indentata (Say, 1823)	The only taxon listed is *Retinella* (*Glyphyalinia*) *indentata paucilirata* (Morelet, 1851). The authors state that this subspecies intergrades in eastern U.S. with nominate *G. i. indentata*.
***Hawaiia minuscula* (Binney, 1841)**	*Hawaiia minuscula* (Binney, 1841)
Striatura meridionalis (Pilsbry & Ferriss, 1906)	*Striatura meridionalis* (Pilsbry & Ferriss, 1906)
***Zonitoides arboreus* (Say, 1817)**	*Zonitoides arboreus* (Say, 1817)
VITRINIDAE	
Vitrina pellucida (Müller, 1774) [variety *alaskana* Dall, 1905, not listed by Turgeon et al. (1988)]	*Vitrina pellucida alaskana* Dall, 1905 [only this variety is listed]
POLYGYRACEA	
THYSANOPHORIDAE	
Thysanophora hornii (Gabb, 1866)	*Thysanophora hornii* (Gabb, 1866)
Microphysula ingersollii (Bland, 1875)	*Microphysula ingersollii* (Bland, 1875)
HELICACEA	
OREOHELICIDAE	
***Oreohelix strigosa* (Gould, 1846)**	*Oreohelix* (*Oreohelix*) *strigosa depressa* (Cockerell, 1890)[3]
***Oreohelix yavapai* Pilsbry, 1905** The following varieties, not listed by Turgeon et al. (1988), have been placed in synonymy with *O. yavapai*:	*Oreohelix* (*Oreohelix*) *yavapai* Pilsbry, 1905
***profundorum* Pilsbry & Ferriss, 1911**	*Oreohelix* (*Oreohelix*) *yavapai profundorum* Pilsbry & Ferriss, 1911
***extremitatis* Pilsbry & Ferriss, 1911**	*Oreohelix* (*Oreohelix*) *yavapai extremitatis* Pilsbry & Ferriss, 1911

Table 10 (cont'd)

Taxon (bold face indicates taxon is reported from the Grand Canyon, including taxa reported herein for the first time)	**Identifications of Bequaert & Miller (1973)**
Oreohelix yavapai, subspp. (cont'd)	
***angelica* Pilsbry & Ferriss, 1911**	*Oreohelix* (*Oreohelix*) *yavapai extremitatis* Pilsbry & Ferriss, 1911
***fortis* Cockerell, 1927**	*Oreohelix* (*Oreohelix*) *yavapai extremitatis* Pilsbry & Ferriss, 1911
HELMINTHOGLYPTIDAE	
	S. BINNEYI COMPLEX
***Sonorella coloradoensis* (Stearns, 1890)**	*Sonorella coloradoensis coloradoensis* (Stearns, 1890)
	S. HACHITANA COMPLEX
Sonorella coltoniana Pilsbry, 1939	*Sonorella coltoniana* Pilsbry, 1939
Sonorella compar "Pilsbry" Pilsbry & Ferriss, 1919 [nom. nov. pro *S. hachitana ashmuni* Pilsbry, 1905]	*Sonorella compar* Pilsbry in Pilsbry & Ferriss, 1919
***Sonorella reederi* Miller, 1984**	

[1] This table lists taxa of mollusks which do, or potentially could, occur in the Grand Canyon, based on biogeographic distributions reported in the literature and seen in collections of the Academy of Natural Sciences of Philadelphia. Higher taxa and binomens listed in the first column are as arranged by Turgeon et al. (1988).

[2] Physidae from the Grand Canyon are in this report identified only as *Physella* spp.

[3] *Oreohelix strigosa depressa* (Cockerell) is the only variety of *O. strigosa* listed by Bequaert & Miller (1973); they indicate that the nominate *O. s. strigosa* (Gould) occurs neither in Arizona nor in the Southwestern Molluscan Province.

(Pilsbry, 1948, and ANSP collection). The Kanab Creek occurrence is on the northern boundary of the Southwestern Molluscan Province (see Bequaert & Miller, 1973:8), and the Vasey's Paradise occurrence more certainly establishes the genus in this province.

Zonitidae

Bequaert & Miller (1973:146) state that *Zonitoides arboreus* (Say, 1817) is usually found above 5,000 ft, "below 5,000 ft only as introductions by man under artificial conditions of moisture and shelter." At Thunder River the species appears at its confluence with Tapeats Creek, at an elevation of about 2,500 ft, in sheltered natural conditions.

Oreohelicidae

The biogeographic range of *Oreohelix* is throughout the Rocky Mountain region; its western boundary passes from Nevada into the Arizona Strip, turns southward and crosses the Colorado River in the Toroweap area. The Thunder River occurrences of *O. strigosa* (Gould, 1846), reported here for the first time, are close to the western boundary for the genus.

Helminthoglyptidae

Sonorella reederi Miller, 1984, was described from specimens found near Rampart Cave, in westernmost Grand Canyon overlooking Lake Mead. The limit of eastward extension of this Lower Sonoran life zone species in the Grand Canyon is unknown. Malacological investigations in the western Grand Canyon should make this determination (*fide* W. B. Miller, written commun., 1990).

Stylommatophora undet.

Slugs found at the confluence of Thunder River and Tapeats Creek were not identified before decomposing, and a subsequent collection was not yet available to the authors at the time of this writing. They are probably of the family Limacidae; if so, the most likely member to occur at the Grand Canyon is the cosmopolitan *Deroceras laeve* (Müller, 1774). If it is this species, it is known to occur as a native in Arizona between 4,500 and 8,000 ft; Bequaert & Miller (1973:149) add, "at lower elevations in cultivated areas." They were found at about 2,500 ft at Thunder River and are the first record of slugs from inside the Grand Canyon.

CONCLUSIONS

Data do not exist for the identity, distribution, or productivity of the malacofauna in the natural regime of the Colorado River before Glen Canyon Dam. In the new regime, this fauna is in an uncertain state of equilibrium with ecological characteristics, for which data are not available. The fauna of aquatic mollusks has not established itself in the Colorado River mainstream below Lees Ferry, but inhabits perennially wet tributaries through the length of the canyon. Bivalvia are known at this time only from the Colorado River in the area above Lees Ferry; if they are not native to the Colorado River here they may have been artificially introduced when the fishery was stocked with invertebrate food sources for the stocked fish, or they may have been introduced by natural mechanisms into the new river regime after 1963. Terrestrial gastropods have not been observed along the riverbanks within or above the former high-water range of the river, with the singular exception of the diverse community inhabiting Vasey's Paradise. These gastropods inhabit the river corridor in wet tributaries, but the extent of their modern ranges is unknown. Land snails are known from all elevations of the canyon and surrounding plateaus, and terrestrial forms preferring wet areas are found in tributaries even in close proximity to the Colorado River. Their apparent absence along the river itself (with the exception of a single species described by Miller, 1984, from westernmost Grand Canyon), even above the high water zone, may be due to non-collection or to a failure to yet colonize the new, more stable, post-dam riparian environment along the river banks.

Rates of riverine distribution of aquatic gastropods between tributaries may be accelerated above natural rates by frequent inundation of tributary mouths, followed by downstream transportation of individuals and eggs and redeposition in other tributary mouths. In the new river regime of perenially cold, clearer water than that of the old regime, mortality of transported individuals in the river may be less than seems likely to have been the case in the once more heavily silted water. Inundation in the new regime likewise may have some negative impact on molluscan communities, particularly in the lower extremities of the tributaries; frequent inundation may wash out redeposited individuals and eggs prior to their integration into the community of the tributary. The balance between these aspects of riverine distribution is unquantified at this time for lack of previous data. Natural mechanisms of distribution other than by riverine transport and redeposition are generally unknown for these mollusks; this is also true in the Grand Canyon. The provenance of the aquatic gastropods of the Colorado River corridor is uncertain. If they are native to the Grand Canyon, as is probable, they may also have benefited from interbreeding with descendents of the individuals that had been artificially stocked in the fishery above Lees Ferry between 1966 and 1969.

Redefined flows from the Glen Canyon Dam powerplant will likely affect the distribution and productivity of mollusks in the river corridor. Whether the overall effect will be beneficial or detrimental are unknown since there is no baseline study of the subject. Any influences these flows will have on the indigenous fauna and flora of the river corridor will also affect the malacofauna. More infrequent inundation, or more carefully controlled rates of change in river level, could benefit the populations by decreasing the number of individuals or eggs washed out of tributary mouths. Even so, wash-outs of individuals and egg masses from tributaries into the Colorado River will remain at a higher frequency now than it must have been in the natural river regime. Changes of algal production in tributaries, when affected by river inundation, will influence the aquatic molluscan communities of the lower extremities of tributaries. Changes to vegetational diversity or distribution, concordant with subsequent influences on indigenous faunal predators of the mollusks, will likewise have an unknown effect on the malacofauna. Terrestrial mollusks also will be indirectly affected by any widespread or localized changes in their vegetational habitat.

SUGGESTIONS FOR FURTHER WORK

The distribution and diversity of the Grand Canyon malacofauna is an unexplored aspect of the region's biology. The degree of bioecological interaction between a controlled, limnologically altered river with populations of native and introduced mollusks in a wilderness setting are unknown. Dynamics of productivity and dispersal in a riparian setting of a semiarid desert are not well understood, and the Colorado River through the Grand Canyon and its tributaries, with their transition through successive life zones, provides a linearly long but areally restricted locality for such investigations. The mollusks are not in themselves known to be necessary for the productivity of animals that live in the Grand Canyon, nor is it a staple in the diet most of those animals. Just how important they are in the cycle of life and post mortem decay in the Grand Canyon ecosystem needs to be more closely studied. Likewise, correlations need to be analyzed between diversity, abundance, and productivity of the mollusks, versus physical, chemical, and biological components at each locality.

The mechanisms of distribution of both aquatic and terrestrial mollusks of the Grand Canyon are not understood. Aquatic mollusks may play an unrecognized role in the aquatic ecosystem of the Colorado River corridor, perhaps also that of the river itself, and these factors may have a feedback effect on the mechanisms of distribution of these animals. The processes by which the tributaries are colonized need to be understood, and the limits of colonization in these tributaries need to be mapped. Inhabitation of the lower ends only of tributaries would be an indication of dispersal primarily by the Colorado River; both the beneficial and negative impacts of the varying flow regime of the river on distribution, and subsequent impacts on productivity, need to be documented. More widely spread inhabitation in tributaries would be an indication both of colonization from river-transported mollusks and of their opportunistic advancement upstream along tributaries. Occurrences above and below physical barriers such as waterfalls would be an indication of distribution by other fauna, or an introduction of mollusks (again by other fauna) more toward the source of the tributary. An experimental analysis of the physical mechanisms of aquatic dispersal in the Colorado River and in tributaries would benefit studies of distribution of organisms which individually have limited mobililty.

Molluscan communities of wet tributaries may in some places serve as locally important food sources for indigenous fauna. In the Colorado River corridor, abundant other primary food sources are available to many animals; thus the small fraction of mollusks that has been reported in the diets of some of these animals may be related to the abundance of more suitable food. In the tributaries the streamside resources are often less abundant and less widely distributed than they are in the river corridor, and the opportunities for discovery and consumption of food are less there than they are in the river corridor. In this way the molluscan fauna could be of greater importance to the food chain of tributary communities than they are in the river corridor. In this sense, the river would be an important element in intermixing genetic populations of aquatic mollusks. Similarly, the river corridor supports specific habitats for avian, reptilian, and mammalian faunas, all of which could contribute to the transport of terrestrial mollusks—individuals and eggs—between favorable molluscan habitats; in this way the river again could effect the intermixture of genetic material among molluscan populations.

Microcommunities of mollusks are common in the molluscan world. Riparian distributions are one example, wherein suitable habitats are not always colonized; reproducing colonies of mollusks are not always homogeneously distributed, thus the occurrence of some species can be overlooked by casual or areally limited reconnaissances. A more pointed example is the faunal and vegetational community of a spring pour-out; in many places certainly molluscan groups will usually be found only in close proximity to the spring, if not in the spring itself. An example of this malacofauna is in the Hydrobiidae, a family of tiny aquatic gastropods that usually comprise a fauna that inhabits spring mouths that, when they are found, occur in large numbers. They are reported from around the periphery of the Grand Canyon region (Hershler & Landye, 1988), but no concerted effort has been made to find them at stream sources in the Grand Canyon. Obviously, this is mostly due to the logistical problems of access to the spring area and, once there, sometimes to the pour-out itself.

The distribution of colonies of terrestrial gastropods, particularly of groups that live in semiarid conditions of talus and cliff faces, is an aspect of Grand Canyon malacology not mentioned since Pilsbry & Ferriss' (1911) work that included a few observations on the subject. Some terrestrial gastropods may also play unrecognized roles in the trophic food web of the desert inner canyon, particularly as sources of energy and water to small foragers. Local races of some terrestrial gastropods are extremely limited in distribution (Smith, 1970); some may be determined to be unique in the Grand Canyon and their occurrence in the Colorado River corridor needs to be documented. Logistical condsiderations are again a problem in making these determinations as many species are subterranean in habit, living in talus, and although they are colonial the colonies are not homogeneously distributed. Various measurements of terrestrial gastropod habitats in the semiarid inner canyon also need to be documented, as even such outwardly mundane characters as slope aspect and slope angle, in addition to usual considerations such as altitude, vegetation type and cover, are necessary to the understanding of ecological requirements and interactions of these animals (for example, see Dillon, 1980).

Productivity of molluscan communities in different tributaries, measured over the course of seasons and molluscan lives, is an unresolved aspect of the Grand Canyon ecosystem. Both generalized and specific interactions of these animals with the rest of the fauna and flora—terrestrial and aquatic, living and dead—are unknown. The Grand Canyon and the Colorado River provide a reasonably well protected area, politically and in terms of human impact, for long-term studies of various molluscan attributes in semiarid and desert riparian ecosystems. The mainstream Colorado River corridor and dozens of tributaries of varying geological, biological, and climatological characters (which in themselves interrelate) combine in one largely wilderness area to provide an excellent locale for a variety of molluscan studies on subjects for which existing knowledge is scant or absent. Combined also with studies conducted on adjacent plateaus, significant contributions could be realized toward understanding aquatic and terrestrial mollusks in temperate to desert conditions in a geographically contiguous framework of limited areal extent, parts of which have experienced impacts of various degrees by humans. Variations in the level of productivity downstream along the Colorado River could indicate some independence from the riverine environment, in which the productivity of aquatic invertebrates decreases downstream due to the increasing sediment load in the river.

Logistical difficulties (including financial considerations) of long-term studies in this area are the only negative aspect of these suggestions for further work. A good starting point would be well-documented trans-canyon surveys along the Colorado River during different seasons; time is necessary to explore tributaries to their sources as well as riverside areas through the length of the canyon. The present report documents the diversity and distribution of mollusks recorded mostly during one summer survey for which fast reconnaissances were made in selected tributaries and riverside localites. A similarly well-documented cross-canyon survey, repeating the 1906 and 1909 expeditions of Pilsbry, Ferriss, and Daniels, would be a valuable contribution toward understanding present-day regional distributions of mollusks. Comparisons with material collected nearly a century ago might be valuable toward understanding some of the human impacts on the study area, an investigation unfortunately not possible with the mollusks of the river corridor.

The Grand Canyon West of Diamond Creek

Virtually no malacological work has been done west of Diamond Creek (Mile 225.7) along the remaining hydrodynamically natural stretch of the Colorado River to about Separation Canyon (Mile 239.5) and along the impoundment of Hoover Dam (Lake Mead) between there and the end of the Grand Canyon at the Grand Wash Cliffs (Mile 279). The only previous reports of mollusks in this stretch of the river are the casual mention of "Physidae" at Bridge Canyon (Mile 235.2; Carothers & Minckley, 1981), and the description of a new species of *Sonorella* (Helminthoglyptidae) from near Rampart Cave (Mile 275.0; Miller, 1984). A reconnaissance in this stretch of the Colorado is necessary to complement the information gathered between Lees Ferry and Diamond Creek, and all of the considerations for further study are also applicable to this river stretch.

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